

# Diet composition of Baltic ringed (*Pusa hispida botnica*) and grey seals (*Halichoerus grypus*) in Finland



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May 2019  
In association with:



Tiedekunta – Fakultet – Faculty Bio ja ympäristötieteellinen		Koulutusohjelma – Utbildningsprogram – Degree Programme Ympäristömuutoksen ja globaalin kestävyuden maisteriohjelma	
Tekijä – Författare – Author Monica Mehtonen			
Työn nimi – Arbetets titel – Title Diet composition of Baltic ringed ( <i>Pusa hispida botnica</i> ) and grey seals ( <i>Halichoerus grypus</i> ) in Finland			
Oppiaine/Opintosuunta – Läroämne/Studieinriktning – Subject/Study track  Ympäristömuutos			
Työn laji – Arbetets art – Level Maisterintutkielma		Aika – Datum – Month and year 05/2019	Sivumäärä – Sidoantal – Number of pages 51
Tiivistelmä – Referat – Abstract  <p>The Baltic ringed (<i>Pusa hispida botnica</i>) and grey seal (<i>Halichoerus grypus</i>) populations have experienced dramatic changes in their abundances since the early 20<sup>th</sup> century, when their populations were much larger than today but since then have declined due to over exploitation and reproductive challenges linked to environmental pollutants. Both populations have however, begun to recover, and their numbers have increased since the 1970s. This increase has led to more seal-inflicted damages to coastal fisheries resulting in the demand to control their populations. In Finland, fishermen have reported significant economic losses, and many consider seals as the main threat to their livelihood. However, our knowledge on the diet composition and foraging behaviour of Baltic ringed and grey seals in Finnish sea area is lacking. In order to achieve sustainable seal management, more information on their diet is thus needed. Therefore, to shed light on the diet composition of Baltic seals in Finland, I examined the stomach contents from 156 ringed and 73 grey seals collected in 2017 across the Finnish sea area. Furthermore, I analysed dietary differences between demographic factors (i.e. age and sex), and seals from different geographic regions. A total of 15 prey taxa, of which 13 fish species or groups were identified. Ringed seal diet was dominated by benthic isopod <i>Saduria entomon</i> that was recovered from over half of the stomachs. In addition to <i>Saduria entomon</i>, herring (<i>Clupea harengus</i>) were the most important fish species consumed. Other important prey were gobies (<i>Gobiidae</i>), smelt (<i>Osmerus eperlanus</i>) and common whitefish (<i>Coregonus lavaretus</i>). In terms of biomass, common whitefish became the most important prey whereas in numbers gobies dominated the diet. For grey seals, herring were the most common and numerous prey consumed that made up most of their diet. Other common species were sprat (<i>Sprattus sprattus</i>) and smelt. Other prey did not contribute substantially to grey seal diet. Additionally, the results of this study showed differences in diet composition between seals of different age and sex.</p> <p>Itämerennorpan (<i>Pusa hispida botnica</i>) ja hallin (<i>Halichoerus grypus</i>) populaatiot ovat kokeneet dramaattisia muutoksia Itämeressä 1900-luvun alusta lähtien, jolloin niiden kannat olivat paljon suuremmat kuin nykyään, mutta jotka ovat sen jälkeen pienentyneet liiallisen pyynnin ja ympäristömyrkyjen aiheuttamien lisääntymisongelmien takia. Molemmat populaatiot ovat kuitenkin alkaneet elpyä ja hylkeiden määrä onkin ollut kasvussa 1970-luvulta lähtien. Kasvaneet hyljekannat ovat johtaneet rannikkokalastukselle aiheutuvien vahinkojen lisääntymiseen ja sen myötä vaatimuksiin rajoittaa hyljekantoja. Suomessa kalastajat ovat ilmoittaneet merkittäviä taloudellisia tappioita ja monet pitävätkin hylkeitä suurimpana uhkana toimeentulolleen. Itämerennorpan ja hallin ruokavalion koostumuksesta ja ruokailutottumuksista Suomen merialueilla tiedetään kuitenkin vain vähän. Kestävän hyljekannanhoidon saavuttamiseksi, tarvitaankin niiden ruokavaliosta lisää ajankohtaista tietoa. Tämän vuoksi tutkin vuonna 2017 Suomen merialueilla metsästettyjen 156 itämerennorpan ja 73 hallin mahan sisällön. Lisäksi tutkin demografisten tekijöiden (iän ja sukupuolen) ja eri alkuperäalueiden aiheuttamia eroja hylkeiden ruokavalioon. Kaiken kaikkiaan 15 saalisryhmää, joista 13 oli kalalajeja – tai ryhmiä tunnistettiin. Itämerennorpan ruokavaliota hallitsi kilkki (<i>Saduria entomon</i>), jota esiintyi yli puolessa kaikista mahoista. Kilkin jälkeen, tärkein saalislaji oli silakka (<i>Clupea harengus</i>). Muita tärkeitä lajeja olivat tokot (<i>Gobiidae</i>), kuore (<i>Osmerus eperlanus</i>) ja siika (<i>Coregonus lavaretus</i>). Biomassan osalta tärkein laji oli siika, kun taas lukumäärällisesti ruokavaliota hallitsivat tokot. Hallien yleisin ja runsaslukuisin saalislaji oli silakka. Muita yleisiä lajeja olivat kilohaili (<i>Sprattus sprattus</i>) ja kuore. Muiden lajien merkitys hallin ravinnossa oli pieni. Tämän tutkimuksen tulokset osoittivat lisäksi eroja eri ikäisten ja sukupuolta olevien hylkeiden ruokavaliossa.</p>			
Avainsanat – Nyckelord – Keywords Ringed seal, grey seal, Baltic Sea			
Ohjaaja tai ohjaajat –Handledare – Supervisor or supervisors Kaarina Kauhala, Jukka Horppila			
Säilytyspaikka – Förvaringställe – Where deposited Helsingin yliopisto			
Muita tietoja – Övriga uppgifter – Additional information			

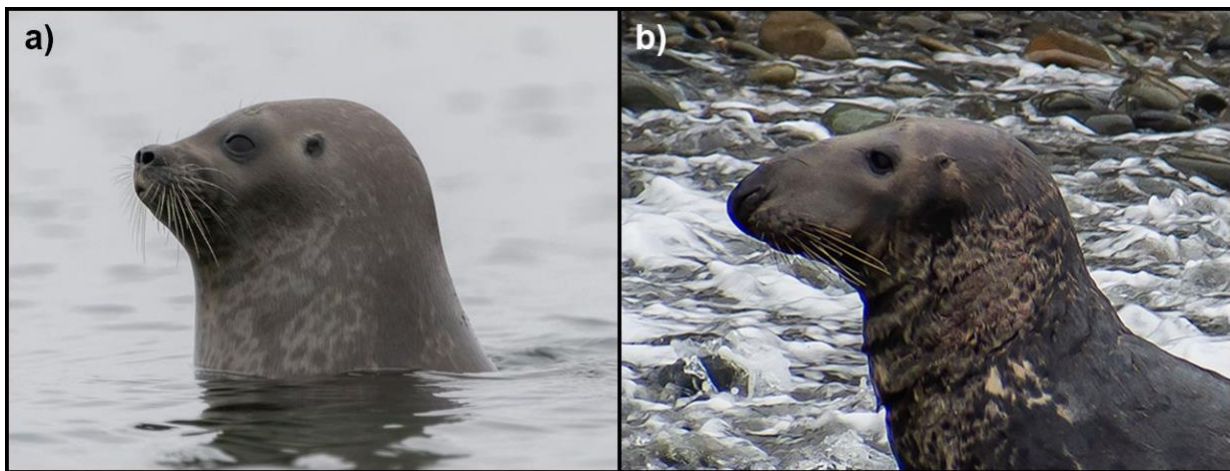
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## 1. Introduction

### 1.1. Baltic ringed and grey seal morphology

The Baltic ringed seal (*Pusa hispida botnica*) and the grey seal (*Halichoerus grypus*) are among the 19 species belonging to the family Phocidae (true seals), also known as the “earless” seals due to the lack of pinnae (external ears) in this family (Martin and Reeves 2002). They also share such characteristics as a unique karyotype ( $2n=32$ ) and white natal fur (lanugo) (Hammill 2009), as well as short haired fore-flippers and non-rotatable hind-flippers, which result in restricted ability to move on ice or land (Martin and Reeves 2002). Both seals have flexible, streamlined bodies that enable rapid swimming movements (Bonner 1981, Bowen *et al.* 2003) and a thick subcutaneous blubber layer that provides protection and insulation, as well as assisting in hydro-dynamic locomotion (Worthy 1991, Martin and Reeves 2002). In addition, they have differentiated teeth and eat flesh alongside other carnivores (Martin and Reeves 2002). Despite these similarities, Baltic ringed and grey seals can easily be distinguished from each other based on their size and morphology (Figure 1).



**Figure 1.** Photographs of a) Baltic ringed seal (*Pusa hispida botnica*) with characteristic small rounded head, short neck and cat-like facial features and b) grey seal (*Halichoerus grypus*) with a characteristic long face with wide and convex muzzle and long and scarred neck. (Photograph a: Tolvanen 2017; photograph b: Mehtonen 2018).

The ringed seal is one of the smallest pinnipeds in the world, with adults growing up to 1.3 - 1.5 m in length and weighing up to 100 kg prior to breeding (Hammill 2009). There are five recognized subspecies of ringed seal, of which the Baltic ringed seal is the largest, with mature seals reaching a maximum length of 1.75 m and an average pre' breeding weight of 93 kg. Both sexes are similar in size: males (bulls) are only around 3% larger and 4 to 5 cm longer than females (cows) (Helle 1983, Hammill 2009). They are, however, considerably smaller than grey seals,

which are the largest species in the Baltic Sea (Lundström *et al.* 2007). Their facial features and expressions are somewhat cat-like, with a proportionately short neck, small rounded head, short muzzle and large forward-facing eyes (Figure 1a) (Shirihai and Jarrett 2006). They are characterized by their pelage, which is covered with a distinct ringed pattern. The dorsal side is usually dark grey or black with pale silvery rings, or silvery-grey with black spots, whereas the ventral area is light grey and often without rings or spots (Hammill 2009). Furthermore, ringed seals have small fore-flippers with strong claws, which are used to excavate and maintain breathing holes in the land-fast and pack ice (Martin and Reeves 2002, Hammill 2009).

Grey seals are the largest of the three species found in the Baltic Sea (Lundström *et al.* 2007). They exhibit sexual dimorphism, with males around 20% longer and 50% heavier than females (Bowen *et al.* 2003). Adult males can reach a maximum length of 3 m and weigh up to 300 kg. Females are smaller, with a maximum length of 2 m and weight of 200 kg (Hall and Thompson 2009). In the Baltic Sea, grey seals are smaller: mature males typically weigh between 160 and 220 kg and females around 150 kg (Helle 1983). The pelage on the dorsal side is mainly dark grey with irregular spots or blotches, whereas the ventral side is lighter grey and spotty (Shirihai and Jarrett 2006). Additionally, male grey seals have a generally darker and more uniformly colored pelage, a very large and downcurved muzzle and a thick, heavily wrinkled and scarred neck. In comparison, females are more lightly colored and usually have a darker dorsal side compared to the ventral side. Furthermore, females have a smaller and narrower head with finer facial features (Shirihai and Jarrett 2006, Hall and Thompson 2009). Both sexes, however, have a long face with distinct wide and convex muzzle and widespread nostrils (Figure 1b) (Miller and Boness 1979), which make them easily distinguished from ringed seals.

## **1.2. Distribution and abundance of Baltic ringed and grey seals**

The ringed seal is a circumpolar species, occurring in seasonally ice covered (Lowry 2016) marine and freshwater areas across the Northern Hemisphere. There are five geographically isolated subspecies of ringed seals: 1) The *P.h. hispida*, which is the most broadly distributed subspecies, is found throughout the northern areas of Russia, Svalbard, Greenland, Alaska and Canada (including freshwater lakes in northern Canada), 2) The *P.h. ladogensis*, found only in Lake Ladoga, a freshwater lake in western Russia, 3) The *P.h. saimensis*, occurring in interconnected lakes in southeast of Finland, 4) The *P.h. ochotensis*, occurring in the Sea of Okhotsk, in the western Pacific Ocean, and 5) The *P.h. botnica*, found across the northern Baltic Sea (Hammill 2009). Most of the

seals in the Baltic Sea are found in the northern and eastern regions, in the Gulf of Bothnia and Gulf of Finland. Additionally, two other subpopulations occur in the Archipelago Sea and western Estonia (Gulf of Riga and Estonian coastal waters). All four areas are used for resting, breeding and moulting, but their breeding distribution is largely restricted to areas with suitable fast and pack ice (HELCOM 2018a). Therefore, the majority (75%) of the animals occur in the Bothnian Bay, where ice conditions are sufficient, even during mild winters. (Härkönen *et al.* 1998, Kunnasranta 2010). Additionally, the distribution of ringed seals is largely associated with prey availability (Lowry 2016).

Grey seals are distributed across the Atlantic Ocean in three geographically separate populations: 1) The Eastern Atlantic, 2) The Western Atlantic, and 3) The Baltic Sea (Hall and Thompson 2009). Most of the grey seals worldwide (about 45%) can be found in the Eastern population, around the UK and Ireland, with smaller numbers around the northern Europe, Iceland and Faroe Islands (SCOS 2016). In the Western Atlantic, the population is located near the coast of the eastern United States and southern Canada (Cameron 1967), whereas the Baltic population resides and is confined to the Baltic Sea (Harding and Härkönen 1999), where the majority of the animals are found north of the latitude 58°, in the northern and central Baltic proper (Lundström *et al.* 2007, HELCOM 2018b). The main moulting areas can be found in the Bothnian Sea, Archipelago Sea and western Estonia. Additionally, an increasing number of animals are found toward the Kattegat and southwestern Baltic (HELCOM 2018b).

In 2017, around 30 000 grey seals were recorded in the Baltic Sea, of which, 9 600 were observed in Finnish sea area during aerial monitoring. The number of ringed seals that same year was estimated at around 13 600 animals in the Bothnian bay, whilst some hundreds to a thousand animals occurred in other subpopulations (Halkka and Tolvanen 2017, Luke). Not all animals are detected during aerial monitoring, and therefore, the abundance is generally underestimated and the actual number of both species should be assumed higher than the reported figures. Both populations have grown since 1990 (Harding *et al.* 2007) and from the beginning of the 21<sup>st</sup> century the annual growth has been around 5 %. However, the number of observed grey seals in the Finnish sea area has not increased substantially during recent years, despite the currently increasing subpopulation found in the Bothnian Bay (Halkka and Tolvanen 2017, Luke 2017). Globally, the total estimated number of grey seals is between 400,000 and 600,000 animals (Bowen 2016), whereas, around 2.5 to 5 million ringed seals are estimated to occur worldwide (e.g. Helle 1983, Hammill 2009).

### 1.3. Life history of Baltic ringed and grey seals

#### ***Reproduction***

Both Baltic ringed and grey seals reach sexual maturity between the ages of 3 and 7 years, with females generally maturing and breeding earlier than males (Helle 1983, Lowry 2016). Both species are long-lived with ringed seals reaching up to 45 (Hammill 2009) and grey seals up to 40 years (Shirihai and Jarrett 2006). However, the lifespan of female grey seals is usually 10 years longer than that of males (Beck *et al.* 2007). The timing of the breeding season depends on the species and varies between the recognized subspecies and populations. In the Baltic sea, this period takes place in early spring for both species, with females giving birth to a single white covered pup (Hall and Thompson 2009, Hammill 2009) between February and March. The breeding season involves birth, a post-natal nursing period and weaning, followed by polygynous mating, which mainly takes place underwater (also under-ice for ringed seals) (Helle 1983, Kelly *et al.* 2010).

Ringed seals give birth on pack ice, in areas suitable for building liars (e.g. Granlund 1974, Helle 1980, HELCOM 2018a). The highest numbers of animals are found breeding on stable first-year or broken consolidated ice, that traps snow heaps and enables snow drift formation and where building liars is the most practical. Pups are usually born in a subnivean liar, which provides them with protection against predators and unfavorable ambient conditions. Pups, however, are capable of enduring great variations in ambient temperatures, and therefore, it has been suggested that liars are mainly used for protection (Hammill 2009). Additionally, ringed seals abrade a series of breathing- and haul out- holes in the fast ice near the liars (e.g. Hook and Johnels 1972, Helle 1983, HELCOM 2018a) as well as alternative liars, that can be used during lactation. Birth is followed by a nursing period of 3 - 6 weeks (Helle 1983), after which mating occurs at the time of the weaning (Hammill 2009). In the Baltic Sea, mating usually commences 3 - 5 weeks after birth, with males mating with several females. Females undergo an embryonic diapause, with delayed implantation (3 months), followed by a 8-month gestation period (Helle 1983).

In comparison, female grey seals can give birth on either land or ice, but in the Baltic Sea, ice is usually preferred (Helle 1983). During mild winters and weak ice conditions however, grey seals are restricted to breed on land, which has been linked to pup survival rates. It has been suggested that pup mortality rates are associated with birthing site selection, with pups born on land showing higher mortality rates compared to pups born on ice, due to inferior health conditions and

significantly lighter pup mass at weaning (Jüssi *et al.* 2008). Offspring are usually nursed for 2 - 3 weeks, after which they are weaned concurrently as females come into estrus and mate again. In the Baltic Sea, the mating season usually occurs 2 - 4 weeks after birth and involves males mating with multiple females. As among ringed seals, there is a delay in implantation (3 months), which is followed by a 8-month gestation period (Helle 1983).

### ***Moulting***

The annual life cycle of seals includes two main haul-out periods: the breeding and the moulting. After the breeding season, both seals undergo the annual moult in spring, when large numbers of animals aggregate on ice or land. The moulting period usually lasts for a few weeks (Sjöberg 1999) and includes the shedding of the old and the growth of the new fur. This moulting process is imperative for maintaining thermal regulation (Leeney *et al.* 2010). In general, ringed seals tend to be solitary (Hammill 2009) or assemble in smaller colonies, but between April and May (in the Baltic Sea) most animals gather on ice or ice-floats to commence their moult (Helle 1980, Helle 1983). In comparison, grey seals are highly social animals that live in large colonies (Sjöberg 1999) and aggregate on skerries or the last ice-floats to undergo their annual moult between May and June (Helle 1983, Kunnasranta 2010). Pups begin to shed their white natal fur (lanugo) at the time of weaning, after which their first hair coat already resembles the adult pelage (Hall and Thompson 2009, Hammill 2009). When moulting, seals generally lose weight due to the reduced time available for foraging (Boily 1995). This is especially true for female grey seals, that are known to fast during the moulting season and may lose a significant amount (up to 40%) of their initial body weight while hauling out (Hall and Thompson 2009).

### **1.4. Diet of Baltic ringed and grey seals**

#### ***Foraging***

As seal ecology is generally defined by the two main haul-out periods and marine feeding, seals return back into the water to engage in foraging activities after breeding and moulting (Hammill 2009). When hauling out, seals usually do not feed, or their feeding is reduced and therefore they have to rely on the energy reserves stored earlier in the year. It is known that the thickness of the blubber layer varies between seasons, and that it is its thickest prior to breeding. There is also a momentary increase in feeding activity in early summer, when seals begin to deposit fat to replace



the energy reserves lost whilst breeding and moulting (Anderson and Fedak 1985) and to prepare for the next breeding (Helle 1983). These post fasting foraging activities are important for their survival and for the success of the future breeding (Hammond *et al.* 1994). While both the Baltic ringed and grey seal share similar life histories, they use different strategies in supporting the costs of reproduction. Ringed seals are usually considered as income breeders, that do not fast, or whose fasting is only partial during the breeding season (Kelly *et al.* 2010, Young and Ferguson 2013). They store less energy and nutrients prior to breeding than grey seals that in comparison are capital breeders (Bowen *et al.* 2002). Therefore, the significance of reserving energy is greater for grey seals, that fast the entire breeding and moulting season and that fully rely on the fat deposited during the year (Hall and Thompson 2009).

Foraging can occur in coastal or open waters and is dependent on individual preferences. Some individuals prefer foraging near the haul-out sites whereas others perform long-distance foraging migrations or travel shorter localized-distances (e.g. Thompson *et al.* 1996, McConnell *et al.* 1999, Dietz *et al.* 2003, Sinisalo *et al.* 2008, Russell *et al.* 2013, Lundström *et al.* 2014, Oksanen *et al.* 2014, Oksanen *et al.* 2015, Vincent *et al.* 2016). Baltic ringed seals usually forage in coastal areas, with males traveling longer distances than females (Twiss *et al.* 2003). In addition, female foraging is somewhat restricted during the breeding season due to the location of the breeding areas, which are situated in the middle of the land-fast and pack ice (Smith and Stirling 1975). Males typically maintain large under-ice territories and can forage more freely throughout the breeding season. The home range is therefore dependent on the season but also sex, with adult males generally maintaining smaller ( $1 - 13.9 \text{ km}^2$ ) home ranges than females ( $1 - 27.9 \text{ km}^2$ ) (Kelly *et al.* 2010). Grey seals also forage in coastal water but their home ranges in the Baltic Sea can extend to over  $6,000 \text{ km}^2$  (Sjöberg and Ball 2000) and their foraging migrations as far as 150 km away from their haul-out sites (Thompson *et al.* 1996, Kunasranta and Lehtonen 2010). Nevertheless, they tend to stay within  $50 \text{ km}^2$  of their haul-out sites (Sjöberg and Ball 2000). Foraging near the haul-out sites is beneficial because it uses less energy than when traveling longer distances and therefore this reserved energy can instead be used whilst fasting during the breeding and moulting season (McConnell *et al.* 1999).

## **Diet composition**

Both the ringed and the grey seals are opportunistic feeders with generalist diets, that typically prey on the species most abundant at any given time (e.g. Lundstrom *et al.* 2010, Suuronen and Lehtonen, 2012). They are successful top predators that consume a variety of different species. It is known that the diet composition varies between different areas (geographical location, coastal or open water areas), seasons, ages and the sexes. (e.g. Söderberg 1975, Lowry *et al.* 1980, Prime and Hammond 1990, Moulton *et al.* 2002, Lundström *et al.* 2007, Labansen *et al.* 2011).

Baltic ringed seals typically prey on a variety of species including demersal and pelagic fish, crustaceans and isopods such as *Saduria entomon* (e.g. Söderberg 1975, Tormosov and Rezvov 1978, Stenman and Pöyhönen 2005, Sinisalo *et al.* 2006). Some seals prefer benthic to pelagic foraging, although usually alternating between the two (Hjorth Scharff-Olsen *et al.* 2018.) Their diet mainly comprises 12 fish species (Söderberg 1975, Stenman and Pöyhönen 2005), however, a total of 18 fish species have been recorded in a recent study (Sinisalo *et al.* 2006, Hjorth Scharff-Olsen *et al.* 2018). Baltic ringed seals usually consume pelagic schooling fish species, such as herring (*Clupea harengus*) and smelt (*Osmerus eperlanus*), as their predominant food source, however, herring is the most important prey species. Additionally, three-spined stickleback (*Gasterosteus aculeatus*), salmon (*Salmo salar*), and benthic fish such as fourhorn sculpins (*Myoxocephalus quadricornis*) and ruffe (*Gymnocephalus cernuus*) are important prey for Baltic ringed seals as well (e.g. Söderberg 1975, Tormosov and Rezvov 1978, Routti *et al.* 2005, Stenman and Pöyhönen 2005, Sinisalo *et al.* 2006). In general, ringed seals tend to prefer fish over crustaceans (Lundström *et al.* 2014), although a large proportion of open water and young seal diet comprises of crustaceans (Labansen *et al.* 2011, Moulton *et al.* 2002). Furthermore, many authors suggest that the benthic isopod *Saduria entomon* is especially important prey for Baltic ringed seals during breeding and moulting, whilst their proportion as prey during the rest of the year is usually insignificant (Söderberg 1975, Tormosov and Rezvov 1978, Helle 1983).

Grey seals also consume both demersal and benthic fish and in the Baltic Sea and are known to prey on over 20 different species (Söderberg 1975, Pöyhönen 2001). However, Hjorth Scharff-Olsen *et al.* (2018) have recently reported a total of fifty fish species found in grey seal samples collected throughout the Baltic Sea. Unlike ringed seals, grey seals mainly consume fish throughout the year and even though they feed on a variety of species, only few contribute significantly to their diet. As for the ringed seal, herring is the most important prey for grey seals of all ages and makes

up the majority of their diet both in biomass and numbers (Söderberg 1975, Pöyhönen 2001, Stenman and Pöyhönen 2005, Lundström *et al.* 2007, Lundström *et al.* 2010). A large proportion of grey seal diet also comprises of common whitefish (*Coregonus lavaretus*) and sprat (*Sprattus sprattus*) (Lundström *et al.* 2007). Cod (*Gadus morhua*) used to contribute substantially to the grey seal diet in the 1960s and 1970s (Söderberg 1972), until their stocks were depleted and as a result their significance for seals decreased. Nowadays, grey seals rarely catch cod due to the number of cod remaining low. Salmonids, such as Atlantic salmon and sea trout (*Salmo trutta*) are also part of grey seal diet (Söderberg 1975, Stenman and Pöyhönen 2005, Lundström *et al.* 2010), although their importance still remains somewhat unclear (Suuronen and Lehtonen 2012). Other important prey species are cyprinids (*Cyprinidae*), eelpout (*Zoarces viviparus*) and flounder (*Platichthys flesus*). Baltic grey seals are also known to feed on sandeels (*Ammodytes marinus*), smelt (*Osmerus eperlanus*), perch (*Perca fluviatilis*), sculpins (*Cottidae*), burbot (*Lota lota*), ruffle (*Gymnocephalus cernuus*), eel (*Anguilla anguilla*), pike (*Esox lucius*) and gobies (*Gobiidae*) (Lundström *et al.* 2007).

### **1.5. Exploitation and threats to Baltic ringed and grey seals**

Both the Baltic ringed and grey seal have experienced dramatic changes in their abundances since the early 20<sup>th</sup> century, when their populations were much larger than today. Around 190,000 – 220,000 ringed and 88,000 – 100,000 grey seals were estimated to occur in the Baltic Sea in the early 20<sup>th</sup> century. At the end of the 19<sup>th</sup> century, seals were first considered as competitors to the fisheries and an extensive seal hunting was initiated in the Nordic countries, to reduce the populations. In Finland, seal bounties were paid from 1909 to 1918 and again from 1924 until 1975 (Harding and Härkönen 1999). Additionally, as the techniques and tools improved, seal hunting became of higher commercial interest (Summers 1978).

By the 1940s the hunting pressure had already drastically decreased the seal populations and only around 23 000 to 27 000 ringed and 20 000 grey and seals remained. These remaining seal populations were further reduced in the mid-1960s due to sterility and the resulting lowered fertility rates that were both linked to environmental pollutants such as PCB and DDTs in the environment (Bergman and Olsson 1986). Furthermore, environmental toxins slowed the recovery of the seal populations from the 1960s. By the late 1970s both populations had declined to only about 5 000 (ringed seals) and 4 000 (grey seals) individuals (Harding & Härkönen 1999, Harding *et al.* 2007).

During the 1970s, the use of DDTs and PCBs were banned in most of the countries surrounding the Baltic Sea, which has resulted in decreasing pollutant loads followed by the slowly recovery of Baltic seal populations (Bergman 1999, Routti 2009). Seal hunting was also prohibited in the Baltic Sea in 1988, which increased the abundance of seals since after the late 1980s. However, due to the growing seal abundance in the 21<sup>st</sup> century and the resulting increase in seal-inflicted damages to fisheries, seal hunting was re-established in Finland in 1998 for grey seals and in 2015 for ringed seals. (Kauhala *et al.* 2016, Suomen Riistakeskus).

Although the worldwide abundance of both seals is suggested to be increasing, local variation exists between subpopulations. As mentioned earlier, only the Bothnian Bay ringed seal subpopulation is currently increasing, whilst the other subpopulations in the Baltic Sea remain small. Additionally, the number of grey seals in Finland has not increased recently. Both seal species were classified as “Least Concern” by the International Union for Conservation of Nature (IUCN) in 2015 (Härkönen 2016, Härkönen 2015), however, Baltic ringed seals were classified as “Near Threatened” in Finland according to the red list of mammals in 2019 (Liukko *et al.* 2019). This underlines the impact of the various anthropogenic threats seals continue to face including climate change, pollution, habitat degradation, entanglement and bycatch (Morizur *et al.* 1999, Bjørge *et al.* 2002, Allen *et al.* 2012).

#### **1.6. Seal-fishery conflict**

As seals have been considered the main competitors to fisheries since the end of the 19<sup>th</sup> century, the conflict between the two has provoked controversy for years. This seal-fishery conflict has been the topic of intensive public debates since the problem was first recognized but has recently become more prominent due to the growing seal populations (Harding and Härkönen 1999, Lunneryd 2001) and their damaging impacts on the fishing industry (Hansson *et al.* 2017). Foraging seals have been reported to damage fishing gear and catch, reduce fish stocks and the commercial value and health of fish, as well as cause significant catch losses (e.g. Westerberg *et al.* 2000, Kreivi *et al.* 2002, Lunneryd *et al.* 2003, Lehtonen and Suuronen 2004). Furthermore, seals directly compete with the coastal fisheries as they prey on commercially important species (e.g. Konigson *et al.* 2013, Haarder *et al.* 2014, Lunneryd *et al.* 2015, Hansson *et al.* 2017). In general, seals interfere with the coastal trap-net fishery and stationary fishing gear such as trap and fyke nets (Storm *et al.* 2007). They are also known to break and tear the nets, thus releasing fish whilst foraging (Suuronen *et al.* 2006). These seal-inflicted damages have resulted in increased economic losses for the

fishermen and nowadays many of them consider seals as the main threat to their livelihood. In fact, in 2015, over one third of commercial fishermen reported significant seal-inflicted losses with a total estimated loss of 175 tons of fish. The biggest losses were to herring, common whitefish, pike perch and salmon catches (Söderkultalahti 2016). In addition, seals have been frequently listed among the most difficult and persistent problems in the industry (Varjopuro 2011).

In the Baltic Sea, grey seals generally account for most of the damages (Westerberg *et al.* 2000, Kreivi *et al.* 2002, Lunneryd *et al.* 2003, Kauppinen *et al.* 2005), but in the Bothnian Bay, ringed seals are known to cause extensive damages to coastal fisheries (Westerberg *et al.* 2000, Kauppinen *et al.* 2005). Additionally, grey seals have been suggested to reduce salmonid (salmon and sea trout) catches and the number of smolts in the Bothnian Bay (Jounela *et al.* 2006). Although the number of seals is not as high as it was before the over exploitation, the increase in damages caused by the seals has resulted in renewed interest in managing the seal stocks (Harding and Härkönen 1999). Over the years, many mitigation methods have been established in an attempt to reduce these damages. Furthermore, alternative gear and fishing technology have been developed together with more comprehensive management approaches in hopes to mitigate the problem (Varjopuro 2011).

In order to achieve sustainable seal management, more information on their diet composition is needed. Such management plans require comprehensive assessment of the ecosystem role of Baltic seals and also improved understanding on their prey choice and foraging behavior. Therefore, more current information on the overall foraging habits of seals in the Finnish sea area is thus needed. Dietary studies are important in providing such information and therefore, form basis for formulating and implementing sustainable management for both the seals and the fisheries.

### **1.7. Diet studies**

Many of the earlier studies on the diet of Baltic seals were conducted in the late 20<sup>th</sup> century, mainly in the 1960s and 1970s (Söderberg 1972 and 1975, Tormosov and Rezvov 1978), when the fish community composition in the Baltic Sea was different to that of today. Since the 1970s, more diet studies have been carried out, but in the Finnish sea area, more information is still needed.

Additionally, many studies have focused on reconstructing the diet composition of Baltic grey rather than ringed seals (e.g. Lundström *et al.* 2007)

There are many ways of conducting diet studies on seals. Most of these studies have relied on the examination of the gastrointestinal tract content or scats but also on visual observations and the collection of behavioral data (Tollit *et al.* 2010). More recent methods include molecular identification of prey remains using fatty acid signatures, stable isotopes and DNA. Each method has its pros and cons, and the use of combinations of complementary methods is recommended (e.g. Hooker *et al.* 2001, Hammill *et al.* 2005). However, methods providing quantified descriptions of diet (e.g. mass) are generally most useful. Since the recovery of gastrointestinal tract contents enables the identification of prey species and the estimation of prey size and mass percentage (Tollit *et al.* 2010), this method was chosen for this study.

## **1.8. Aims**

As the abundance of Baltic ringed and grey seals has increased during the 21<sup>st</sup> century, so has their negative impact on coastal fisheries in Finland (Harding and Härkönen 1999, Lunneryd 2001, Hansson *et al.* 2017). For this reason, there has been a growing demand to manage the seal stocks in order to mitigate this problem (Harding and Härkönen 1999). Therefore, studying the feeding habits and diet composition of both the ringed and the grey seal in the Finnish sea area is an essential requirement in achieving sustainable and effective seal management. Such management efforts require knowledge on the ecosystem role of Baltic seals today as well as improved understanding on their prey choice and foraging behavior. In addition, seal populations are still recovering from centuries of overexploitation, while facing imminent future threats such as climate change, making seals of ecological and conservational interest. Therefore, in order to formulate conservation efforts that safeguard the future survival of Baltic seals, more current information on their diet is urgently needed. Additionally, as top marine predators, seals act as imperative components in maintaining the food web by regulating the abundance of lower trophic levels (Bowen 1997). Thus, it is important to better understand their current dietary preferences in the Baltic Sea.

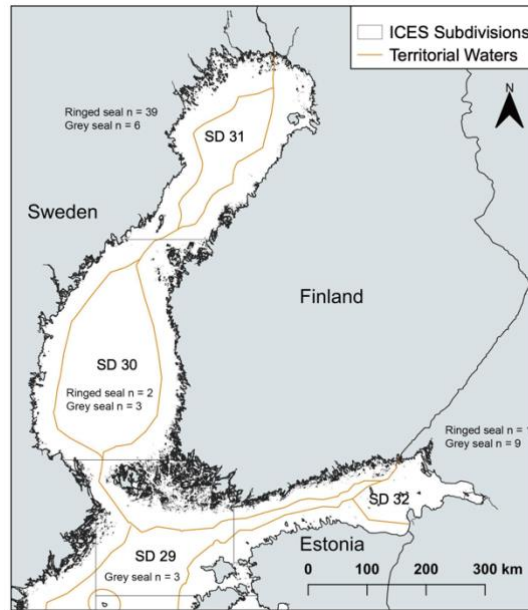
As previously described, earlier studies on the diet composition of Baltic seals have been conducted, but the majority of them focused on grey seals around the entire Baltic Sea (Lundström *et al.* 2007, Lundström *et al.* 2010). Fewer recent studies are available on ringed seals and in the Finnish sea area. Therefore, the aim of this study is to provide data on the diet composition of both the Baltic ringed and the grey seal in Finnish sea area in 2017, based on otoliths and other prey

remains recovered from the stomachs of hunted seals. This study also examines whether demographic factors (i.e. sex and age) (both seals) and geographic region (only grey seals) affect the diet composition. Lastly, this study aims to reconstruct the original size and biomass of consumed prey by ringed seals and analyse whether there were significant differences in the estimated size (length) of the consumed prey between demographic factors (i.e. age and sex)

## **2. Materials and methods**

### **2.1. Study area**

My samples were collected from the Baltic Sea during the annual seal hunting season of 2017. The Baltic Sea is a small intra-continental sea located between the latitudes 54°N and 66°N in the temperate and subarctic zones in northeast Europe (Figure 2). It is one of the largest brackish water bodies (393 000km<sup>2</sup>), consisting of series of shallow basins that are connected to the North Sea only through the narrow Danish Straits in the southeast. In addition, the Baltic Sea is shallow (mean depth 54 m, maximum depth 459 m) and brackish (mean salinity 7‰), with a horizontal salinity gradient or halocline (Leppäranta and Myrberg 2009). This halocline restricts species diversity and since the lowest salinity can be found in the northern regions of the Baltic Sea, most freshwater species occur there. Contrary to this, most marine species are more abundant in the central and Southern Baltic, where the salinity is higher (Ojaveer *et al.* 2010). One of the key characteristics of the Baltic Sea is its annual freezing, which can result in either complete or partial ice coverage during winter (Leppäranta and Myrberg 2009). In addition, the Bothnian Bay can stay covered in ice up to 6 months (Haapala and Alenius 1994). The Baltic Sea is also divided into subdivisions (SD) by the International Council for the Exploration of the Sea (ICES) (Figure 2). These subdivisions around Finland are: 1) The Bothnian Bay (SD 31), 2) The Bothnian Sea and Northern Quark (SD 30), 3) The South West archipelago and Åland (SD 29), and 4) The Gulf of Finland (SD 32) (Kauhala *et al.* 2016).



**Figure 2.** The study area divided into subdivisions by the International Council for the Exploration of the Sea and the territorial waters of Finland, Sweden and Estonia (yellow), where  $n$  is the number of ringed and grey seals containing prey remains, collected from each subdivision.

## 2.2. Seal samples

The samples I analysed were collected by seal hunters between April and July in 2017 and made available by the Nature Resources Institute Finland Luke, that organizes the seal sample collection as part of their annual seal monitoring and research program in Finland. No seals were hunted solely for this study, instead they were hunted legally as part of the annual open seal hunting season. Furthermore, these animals were killed opportunistically and at random, meaning there was no particular selection process. A total of 156 ringed and 73 grey seals were collected and examined. In Finland, ringed seal hunting is only allowed in the Bothnian Bay and the Quark, whereas the hunting area for grey seals encompasses the entire Finnish sea area. Therefore, most of the animals were hunted in the Bothnian Bay, with few grey seals from the other areas. Additionally, the majority of both species were hunted between April and May.

The samples provided to me consisted of the gastrointestinal tracts (stomachs and intestines), genital organs, lower jaw, liver, a piece of blubber and a piece of deltoid muscle taken from each individual seal. Hunters were also asked to provide the hunting locations (GPS



coordinates) as well as measure and weigh the animals and the blubber layer, when possible. The age of the animals was determined from the lower canine teeth by counting the annual incremental lines from histological sections of the cementum (Mansfield 1991), sex from the genital organs and species confirmed from the lower jaw. These determinations were done by the Natural Resources Institute Finland Luke. Stomachs and intestines were separated, placed in plastic bags and stored at -20°C until later examination. As no significant differences in diet composition have been found in previous studies based on whether stomachs or intestines of the seal were examined (Kauhala *et al.* 2011), only stomachs were used in this study.

## **2.2. Prey sample collection and processing**

### ***Recovery of prey remains***

Before the recovery of the consumed prey remains, stomachs were weighed full and later when empty to determine the total mass of the contents. A complete median longitudinal incision from the anterior to the posterior of the seal was then made to access and recover the prey remains. Whole prey items were removed first, separately from the rest of the contents and stored at -20°C in sealed plastic bags. The remaining stomach contents were then rinsed thoroughly several times under running water, over a sieve with a mesh size of 0.5 mm. Both of the longitudinal folds were individually rinsed and examined after which the stomachs were inverted to collect any particles left on the stomach lining. Once all the contents were removed and thoroughly rinsed, the resistant skeletal structures (hard parts) were collected from the sieve and placed in paper bags to dry and be stored (Stenman and Pöyhönen 2005, Tollit *et al.* 2010). Other prey remains (soft tissue) were also removed and stored frozen at -20°C in plastic containers. Additionally, intestinal parasites were collected and stored in 95 % non-denatured ethanol whilst other items, such as rocks and plastics were simply collected and stored.

### ***Identification***

In order to identify the consumed prey, the recovered remains were separated into three major types 1) whole prey, 2) hard parts, including fish otoliths, spines, vertebrae, gill bones, skull parts, pharyngeal teeth and other bones, and 3) other. All prey remains were identified to the lowest taxonomic level possible (species or family) using a stereomicroscopic microscope and a microscope camera that allowed later photo-identification. In general, the identification of prey

remains is based on the morphological features of the prey and different diagnostic structures (i.e. otoliths and other bones) that resist digestion. Usually, whole prey items are recently ingested and have not been exposed to digestion for long and thus can be identified using general guides to species identification. Here, a guide by Yrjölä *et al.* (2016) was used when identifying fish and reference material when identifying isopods and crustaceans. Of the more digested material, otoliths resist mechanical wearing and digestion for the longest time and are therefore, often the main structure used in prey identification. Otoliths are calcium carbonate structures, that are found in the sense organ called the labyrinth, within the cranial cavity of bony fishes (Osteichthyes). The labyrinth is a membranous organ, that is divided into two halves, both consisting of three bags: the utricle, the saccule and the lagena, that each contain one otolith: the lapillus, the sagitta and the asteriscus, respectively. Both of the labyrinth halves are identical in symmetrical fishes and therefore every otolith pair is divided into right and left otolith. Furthermore, they are bilaterally symmetrical and thus, the left and the right otolith can be separated. The largest otolith, the sagitta is species-specific due to its variable and distinctive shape among different species and therefore, is usually used for identification. Within the group Cypriniformes however, the asteriscus is used instead of the sagitta due to its bigger size and a more distinctive shape. The otoliths in this study were identified using guide by Härkönen (1986), together with reference material valid for species in the Baltic Sea. Additionally, other hard parts and prey remains were identified using reference material.

### ***Prey number estimation***

To find out the number of individuals for each prey species at the time of ingestion, all recovered prey remains, except for soft tissue remnants, were counted. Since no existing methods were available for estimating the number of individuals from the soft tissue remains (e.g. digested isopods), only the total mass was calculated. For each seal, the number of individuals per prey species consumed was the sum of the number of whole prey items (i.e. fish with intact skulls and other prey items), other hard parts (e.g. pharyngeal teeth), of which the number of individuals could be determined, and the count of otoliths divided by two. This simple method does not however, take into account the side of the otolith thus giving only an approximate estimate of the number of consumed prey individuals. Therefore, to avoid underestimating the prey number, the side of the otolith (right or left) was taken into account and the more common side used to calculate the minimum number of individuals. In case it was not possible to separate the side of the otolith (i.e. unidentified and too eroded otoliths) the number of individuals was determined from the total

number of otoliths divided by two. Furthermore, all unmatched otoliths were counted and added to the total number of otoliths.

Since the Baltic grey seal diet composition has been reconstructed in previous studies (e.g. Lundström *et al.* 2007) and because the quality and number of the grey seal prey sample was low, the number of prey individuals consumed by grey seals was estimated using the simpler method (i.e. the sum of the number of whole prey items and the count of otoliths divided by two). Contrary to this, similar studies for ringed seals have not been conducted recently and since the size and quality of the prey sample was higher, the more accurate prey number estimation method (i.e. the side of the otolith included) was used for ringed seal samples.

### ***Prey size estimation***

To estimate the original size of the recovered prey at ingestion, the length and width of the otoliths were measured using a stereomicroscopic microscope with an accuracy of 0.04 mm and the size determined to the nearest mm. Some of the otoliths were broken and for those, only the appropriate measurements (i.e. length or width) were taken. Furthermore, whole prey items were also measured and weighed. All measurements here are given in millimeters (mm) and weights in grams (g).

The original size of a fish can be estimated from the size of its otoliths (e.g. Härkönen 1986). Prey size estimation in my thesis was only carried out for the most numerous otoliths recovered from ringed seal stomachs (i.e. gobies, herring, common whitefish and smelt). Since the quality of the otoliths was low, prey size estimation was not possible for prey consumed by grey seals. To calculate the original length and weight of the fish from the otolith measurements, simple linear regression functions:  $y = a + bx$  and power functions:  $y = ax^b$  were used, respectively. The response variable  $y$  in the linear regression function is the fish length in mm (FL),  $a$  is the intercept,  $b$  is the slope and the explanatory variable  $x$  is the otolith length (OL) or width (OW) in millimeters. Additionally, in the power function, the response variable  $y$  is the fish weight (FW) in grams, and  $x$  is either the otolith length or width in millimeters. Since published functions for the prey species recovered from the Baltic ringed seals do not exist, functions presented by Härkönen (1986) and Lundström *et al.* (2007) were applied. Both the linear regression and the power functions for herring were taken from Lundström *et al.* (2007) and for gobies, common whitefish and smelt from Härkönen (1986) (Table 1). These equations are based on the fish species from the northeast Atlantic (Härkönen 1986) and the Baltic Proper (Lundström *et al.* 2007). No significant differences are known of the relative growth rate of the otoliths among fishes from different geographical regions (Härkönen 1986), and therefore the existing functions were applied here. Otolith length is

often used as a size parameter for most fish species. However, in some cases, otolith width can give higher size correlations, thus being more appropriate for some species, especially if the shape of the otolith or its structures are easily broken (e.g. herring, whose otoliths have a very pointed rostrum) (Härkönen 1986). In this study, the otolith length was used for common whitefish and smelt and otolith width for herring and gobies when estimating the original fish length and weight (Table 1). In case the otoliths were only determined to a level higher than the species level (family), the size of the fish was calculated using regression and power functions for those species within the same family that most commonly occur in the study area. Therefore, functions valid for sand goby (*Pomatoschistus minutus*) were used for gobies.

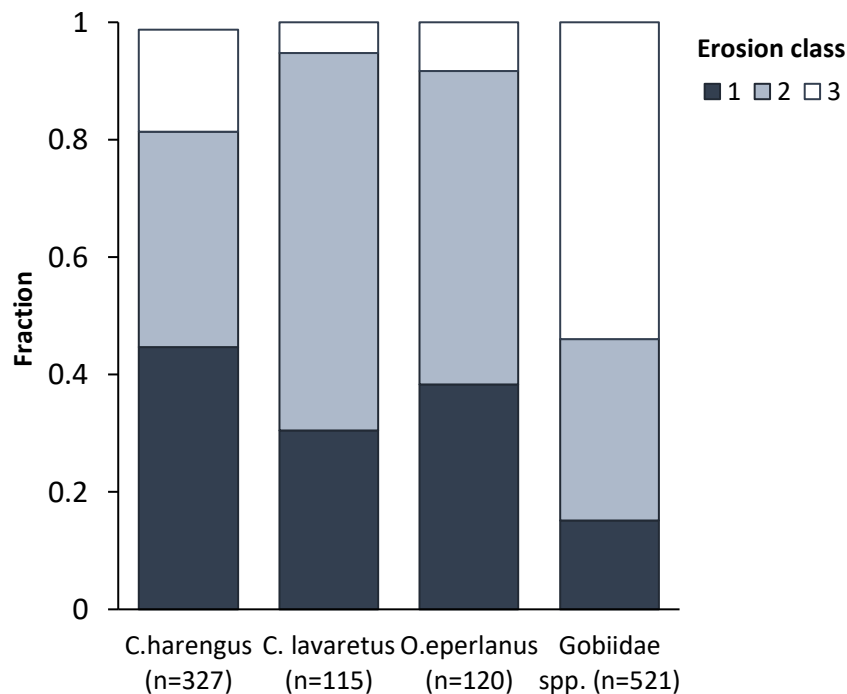
**Table 1.** Linear regression function:  $FL = a + b \cdot OL$  or  $OW$  and power function:  $FL = a \cdot OL$  or  $OW$  used when calculating the original fish length and weight for the most numerous prey species recovered from the ringed seals. Both equations for herring are from Lundström *et al.* (2007) and for gobies, common whitefish and smelt from Härkönen (1986).

Species	Fish length				Fish weight			
	a	b	$r^2$	x	a	b	$r^2$	x
Herring	-49.294	132.44	0.941	OW	3.994	3.798	0.935	OW
Gobies	-23.36	56.94	0.904	OW	0.1677	5.369	0.882	OW
Common whitefish	2.724	48.6	0.963	OL	0.285	3.672	0.976	OL
Smelt	-8.67	32.05	0.960	OL	0.00736	3.719	0.967	OL

### **Size correction**

In order to accurately estimate the original size and biomass of consumed prey from otolith size, digestive erosion needs to be considered. To avoid underestimating the prey size, it is important to determine the original size of the non-eroded otoliths at the time of ingestion (e.g. da Silva and Neilson 1985, Harvey 1989, Pierce and Boyle 1991, Tollit *et al.* 1997). Therefore, a method involving the classification of the otoliths into erosion classes together with estimating size correction factors (SCFs) for the prey species and erosion classes, was applied here. All the recovered otoliths from ringed seals, were classified into three erosion classes according to Tollit *et*

*al.* (1997) The classification of the otoliths is generally based on their surface topography and morphology. In erosion class one (1), otoliths show only minimal erosion with clear sulcuses and other diagnostic structures such as pronounced lobations, throughout the otoliths. Class two (2) otoliths are more eroded, showing overall more rounded and less pointed structures with less lobation and less defined sulcuses. Lastly, in erosion class three (3), otoliths show significantly high signs of erosion with smooth edges and severely altered shape with no sulcuses or lobation (Table 3). After all otoliths were classified, species- and erosion class-specific size correction factors (SCFs) were estimated for the most numerous species in this study (gobies, herring, common whitefish and smelt). The SCFs were calculated for all erosion classes following Lundström *et al.* (2007), as the ratio between the average otolith width or length in erosion class one and erosion class two and three respectively for each species (Lundström *et al.* 2007) (Table 2). Furthermore, SCFs were calculated assuming that class one otoliths were minimally eroded. The fractions of ringed seal otoliths belonging to the three erosion classes for the most numerous species are presented in Figure 3.






**Figure 3.** Fractions of ringed seal otoliths belonging to the three erosion classes for the most numerous species. The total number of otoliths for each species is shown in brackets (n).

**Table 2.** Species and erosion class-specific size correction factors (SFCs) for the most numerous fish species in this study.

Species	Otolith width			Otolith length		
	Erosion class			Erosion class		
	1	2	3	1	2	3
Herring	1.00	1.03	1.05	1.00	1.02	1.02
Common whitefish	1.00	1.08	1.15	1.00	1.11	1.23
Gobies	1.00	1.04	1.07	1.00	1.05	1.09
Smelt	1.00	1.15	1.37	1.00	1.21	1.43

**Table 3.** Following Tollit *et al.* (1997) a summary table showing erosion classes 1, 2 and 3, their descriptions and photographic examples used in this study to classify ringed seal otoliths for size correction procedure. (Photographs: Mehtonen 2019).

Erosion class	Description	Photographic example
Class 1	Minimal erosion	
	Clear lobation on surfaces, margins and rostrums	
	Well defined sulci	
	Original shape	
Class 2	Medium erosion	
	Less clear lobation on surfaces, margins and rostrums	
	Less defined sulci	
	Near original shape	
Class 3	High erosion	
	Minimal-no lobation, smooth edges	
	Low-no sulci	
	Overall altered shape	

## 2.3. Statistical analyses

### ***Categorizing the seal data***

A total of 43 and 21 of the 156 ringed and 73 grey seals respectively, contained prey remains. Seals not containing any prey, were discarded from further analysis. In order to examine possible differences in diet composition between demographic factors (i.e. age and sex), seal sample were divided into two age groups: 1) pups and yearlings (0 - 1 years), and 2) juveniles and mature seals (2 + years), based on the age determined by the Natural Resources Institute Finland Luke.

Additionally, to examine possible differences in diet composition between seals from different geographical regions, grey seals were divided into two groups, based on the ICES subdivision (SD) they were collected from: 1) The Bothnian Bay and Bothnian Sea, and 2) The Archipelago Sea and Gulf of Finland. Furthermore, since the sample size was small ( $n = 21$ ), all seals from SD 31 and SD 30 were pooled in the former and all seals from SD 29 and SD 32 in the latter group (Figure 2 and Figure 5). In addition, most of the ringed seals were hunted in the Bothnian Bay and therefore this analysis was not performed for ringed seals

### ***Diet indices***

To determine the contribution of each prey species to Baltic ringed and grey seal diet, three different indices were calculated: 1) The frequency of occurrence, 2) The relative numerical contribution, and 3) The relative biomass contribution (e.g. Lundström *et al.* 2007, Tollit *et al.* 2010). Frequency of occurrence ( $FO_i$ ) for a prey species was calculated, as the number of stomachs containing the prey species in relation to the total number of stomachs containing prey:  $FO_i = (s_i/s_t) \times 100$ , where  $s_i$  is the number of seals in which the prey taxon  $i$  occurs and  $s_t$  is the total number of seals containing prey remains (Lundström *et al.* 2007). The frequency of occurrence was calculated for all prey species or groups recovered from both seals.

The relative numerical contribution ( $N_i$ ) for a prey species was calculated as the number of individuals of the prey species in relation to the total number of individuals of all prey species ( $N_i$  adds up to a 100, whereas the  $FO_i$  does not). It was calculated as follows:  $N_i = (n_i/n_t) \times 100$ , where  $n_i$  is the total number of individuals of the prey taxon  $i$  and  $n_t$  is the total number of individuals of all taxa (Lundström *et al.* 2007). The relative numerical contribution was calculated only for those prey species recovered from both seals, whose number of prey individuals could be estimated.

The relative biomass contribution ( $B_i$ ), of a prey species was calculated as the total weight of the prey species in relation to the total weight of all species as follows:  $B_i = (b_i/b_t) \times 100$ , where  $b_i$  is the total weight of prey taxon  $i$  and  $b_t$  the total weight of all taxa (Lundström *et al.* 2007). The relative biomass contribution was calculated only for the four most numerous fish species found in ringed seals, whose original size could be estimated, whereas since prey size could not be estimated for prey species found in grey seals, relative biomass contribution could not be calculated.

### ***Diet composition analyses***

I performed statistical analyses using R (R version 3.5.1, “Feather Spray”, R Core Team 2018). Differences in diet composition between demographic factors (i.e. age and sex) (both ringed and grey seals) and geographical regions (grey seals only), were compared using a Chi-square test ( $\chi^2$ ), based on the frequency of occurrence ( $FO_i$ ) of each prey species. In addition, to analyse species richness, a Shannon-Wiener diversity index ( $H$ ) was calculated as follows:

$$H = - \sum P_i (\ln P_i) ,$$

where  $P_i$  is the proportion of each prey taxon in relation to all taxa ( $N_i$ ). Furthermore, to analyse differences in the number of consumed individuals (or total weight in the case of soft tissue remains) between the demographic factors and geographical regions, a Kruskal-Wallis (K-W) test was calculated, since the data were not normally distributed according to the Kolmogorov-Smirnov test (Kauhala *et al.* 2011).

### ***Prey size analysis***

To test whether there were significant differences in the estimated size (length) of the consumed fish between demographic factors (i.e. age and sex), I used a linear mixed model. For this analysis, only otoliths (recovered from ringed seals) of the most numerous fish species (herring, common whitefish, gobies and smelt), and that were corrected with the size correction factors (SCFs) were included ( $n = 1,130$ ). I performed this analysis using R package “lme4” (Bates *et al.* 2019). The log transformed estimated fish lengths  $y_i$  were modelled as normally distributed as follows:

$$\log(y_i) \sim N(\alpha + \beta_{s(i)} + \beta_{a(i)} a_{sp(i)}, \sigma^2) ,$$



where  $\sigma^2$  is the variance of the normal distribution,  $\alpha$  is the intercept,  $\beta_s$  is coefficient of the dummy coded sex of the seal (male),  $\beta_a$  is coefficient of the dummy coded age group of the seal (mature) and  $a_{sp}$  is an *iid* random effect for the fish species with variance  $\sigma_{sp}^2$  ( $a_{sp} \sim N(0, \sigma_{sp}^2)$ ).

### 3. Results

#### 3.1. Sample composition

Of the 156 ringed and 73 grey seals collected in 2017, 43 and 21 contained prey remains, respectively. The majority of the stomachs were empty or contained only few items, however, a total of 1,837 otoliths among other prey were examined. Most of the recovered remains were identified to species level and only cyprinids and gobies to family level. Furthermore, few otoliths ( $n = 3$ ) were not identified due to severe erosion or damage. Both seal samples also included other fish bones, that were only taken into account in case the stomach was otherwise empty. Most of these bones were too eroded to be identified ( $n = 12$ ) and thus were only included in the frequency of occurrence analysis. Furthermore, a total of 16 prey groups, including 14 fish species or families were recorded.

The average age of ringed seals was 5 years (range 0 - 20 years), with the majority (56 %) of them two years old or older (i.e. age group 2), whereas the average age of grey seals was 4 years (range 0 - 18 years), with most of them (62 %) between zero and one years old (i.e. age group 1). For ringed seals, genders were distributed equally, with 51 % being males, whereas, the majority of grey seals were females (81 %) (Table 4). Furthermore, ringed seals were mainly collected from SD 31, the Bothnian Bay (91 %), with only few individuals from other subdivisions, whereas grey seals were scattered across the entire Finnish sea area, with the majority (43 %) of them from SD 32, the Gulf of Finland. After grey seals were divided into two groups based on the geographical region they were collected from, 57 % were from the Archipelago Sea and the Gulf of Finland (2) and 43 % from the Bothnian Bay and the Bothnian Sea (1) (Figure 2, Figure 5). Additionally, the majority of both seals were collected in May.

**Table 4.** Age group and sex of ringed and grey seals containing prey remains.

	Ringed seal n = 43	Grey seal n = 21
<b>Age group</b>		
0 - 1	18 (42 %)	13 (62 %)
2 +	24 (56 %)	8 (38 %)
Unknown	1 (2 %)	
<b>Sex</b>		
Male	22 (51 %)	4 (19 %)
Female	21 (49 %)	17 (81 %)



**Figure 5.** The areas of origin of ringed (n=43) (orange) and grey (n=21) (blue) seals hunted in 2017 that contained prey remains. Few of the seals were hunted in the same location, which is presented on the map as one data point for each location.

### 3.2. Prey occurrence and diet composition

#### *Ringed seal*

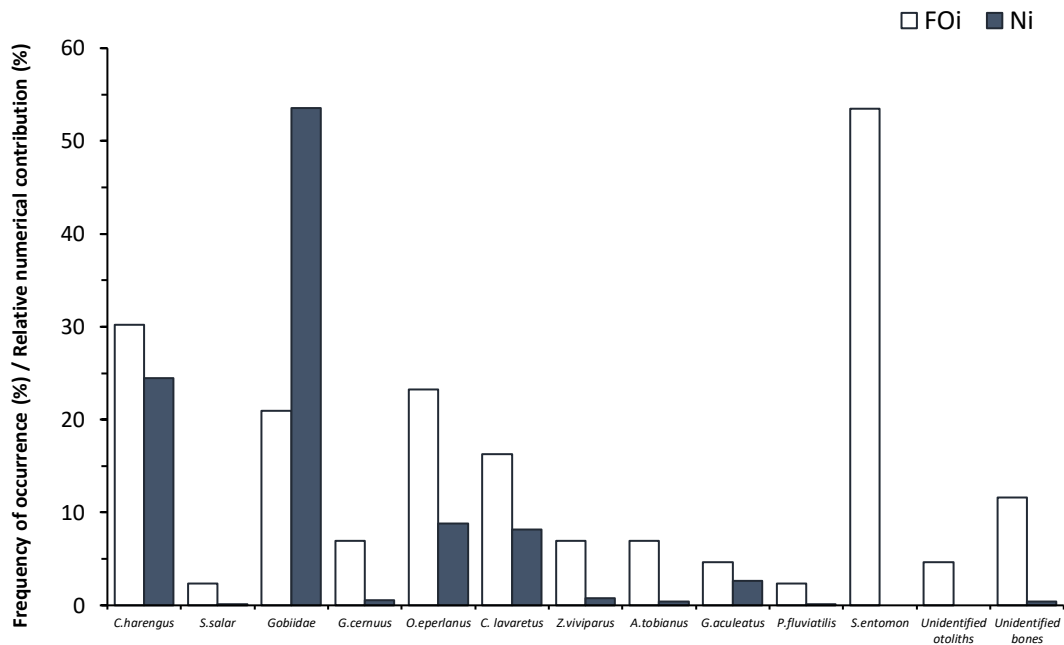
The average wet weight of the stomach contents among ringed seals was 34.9 grams and varied between 0 and 799 grams. Altogether 11 prey taxa, including 10 fish species or groups and in total 1,151 otoliths were recovered. Only two stomachs contained unidentified otoliths ( $n = 3$ ) and five other unidentified fish bones. Of the 43 seals containing prey remains, only two had consumed up to six different species, whereas, more than half of the seals (56 %) had only consumed one species.

The most common prey among ringed seals was benthic isopod (*Saduria entomon*), which occurred in 23 (53 %) stomachs. In total, 1027.11 grams of *Saduria entomon* were recovered, with an average wet weight of 44.66 grams (range 0.05 - 120.04 grams). Herring (*Clupea harengus*) were the most common fish species and altogether 13 seals (30 %) had eaten herring (average 13 herring, range 1 - 39). Furthermore, 23 % of the seals had remnants of smelt (*Osmerus eperlanus*), 21 % of gobies (*Gobiidae spp.*) and 16 % of common whitefish (*Coregonus lavaretus*). In addition, ruffle (*Gymnocephalus cernuus*), sandeel (*Ammodytes tobianus*), and eelpout (*Zoarces viviparus*) were all found in 7 % of the stomachs. Three-spined stickleback (*Gasterosteus aculeatus*) occurred in 5 %, whereas, both perch (*Perca fluviatilis*) and salmon (*Salmo salar*) only in 2 % of the stomachs (Figure 6, Table 5). Altogether 407 gobies, 186 herring, 67 smelt, 62 common whitefish, 20 three-spined stickleback, 6 eelpout, 4 ruffle, 3 sandeel, 1 perch and 1 salmon were recovered from ringed seals (Table 5). Furthermore, even though herring were the most common species, gobies were the most numerous (54 %) with an average of 29 individuals found per seal (range of 1 - 138). After gobies, other numerically important species were herring (24 %), smelt (9 %) and common whitefish (8 %), while no other species contributed more than 3 %.

In addition to prey remains, other items such as plastics, rocks, pieces wood, other plants and metal were recovered from the stomach samples. Seals also contained parasitic worms either attached to their stomach tissue or among the stomach contents. Such parasitic worms were nematode *Contracaecum osculatum* and flatworms that occurred in 23 and 11 stomachs respectively.

**Table 5.** The frequency of occurrence ( $FO_i$ ), relative numerical contribution ( $N_i$ ), number of consumed individuals and number of otoliths for prey taxa recovered from ringed seal stomachs, where n equals the number of seals used for analysis. Additionally, the total weight of *Saduria entomon* is presented here.

Common name	Scientific name	n = 43	n = 25	No. of consumed ind.	No. of otoliths	Weight (g)
		$FO_i$	$N_i$			
Herring	<i>Clupea harengus</i>	30	24	186	327	
Smelt	<i>Osmerus eperlanus</i>	23	9	67	120	
Gobies	<i>Gobiidae</i>	21	54	407	521	
Common whitefish	<i>Coregonus lavaretus</i>	16	8	62	115	
Ruffle	<i>Gymnocephalus cernuus</i>	7	1	4	6	
Sandeel	<i>Ammodytes tobianus</i>	7	0	3	6	
Eelpout	<i>Zoarces viviparus</i>	7	1	6	10	
Three-spined stickleback	<i>Gasterosteus aculeatus</i>	5	3	20	40	
Perch	<i>Perca fluviatilis</i>	2	0	1	2	
Salmon	<i>Salmo salar</i>	2	0	1	1	
Unidentified otolith		5	0	3	3	
Unidentified bones		12	0			
Benthic isopod	<i>Saduria entomon</i>	53	0			1027.11
Total number / total weight (g)				760	1151	1027.11



**Figure 6.** The proportion of ringed seal stomachs containing each prey taxon ( $FO_i$ ) (light bars) and the proportion of each prey taxon in all identified taxa ( $N_i$ ) (dark bars) in the stomachs of ringed seals hunted in 2017.

## **Grey seal**

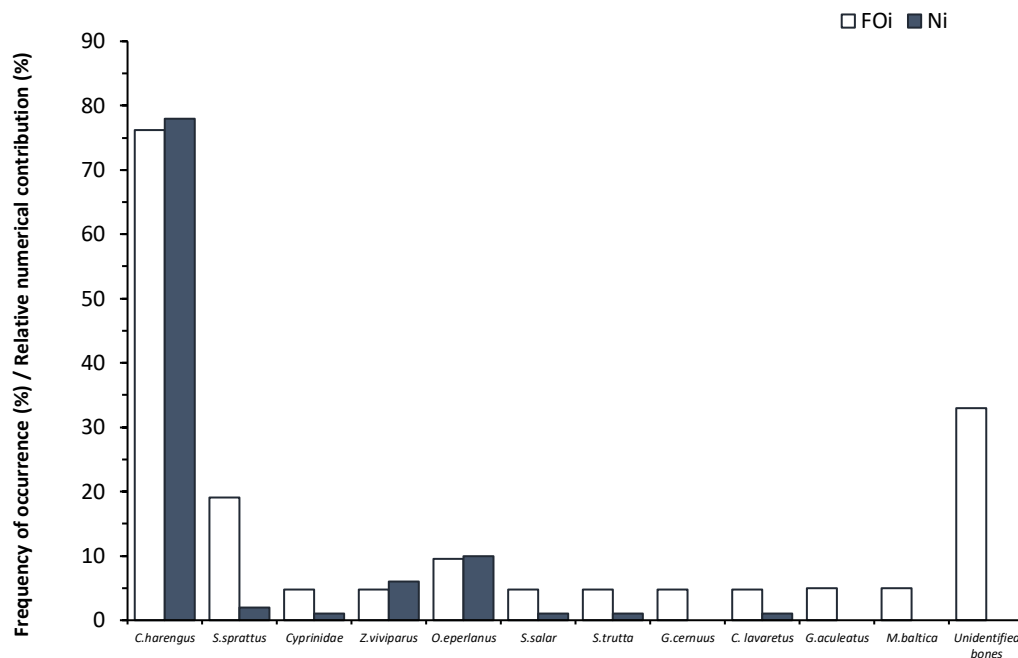
The average wet weight of the stomach contents among grey seals was 67.5 grams and varied between 0 and 1469 grams. In total 11 prey taxa including 10 fish species were recovered. Altogether 686 otoliths representing 350 fish individuals were examined and only 7 fish bones (other than otoliths) were not identified. Of the 21 seals containing prey remains only 1 seal had eaten up to 6 different species while more than half of the seals (57 %) had only consumed 1 species.

The most common (76 %) and the most numerous (78 %) species eaten were herring that occurred in 16 of the 21 grey seal stomachs (average 16 herring per seal, range 0 - 79). After herring, sprat (*Sprattus sprattus*) and smelt were the most common species, occurring in 19 % and 10 % of the stomachs respectively. Other species recovered were eelpout, salmon, trout (*Salmo trutta*), ruffle, three-spined stickleback and common whitefish, which were all consumed by one seal (5 %). Additionally, cyprinids (*Cyprinidae spp.*) were also found from one stomach only (5 %). Furthermore, a marine bivalve mollusk Baltic macoma (*Macoma balthica*) was also found in one stomach (5 %) (Table 6, Figure 7). In total 274 herring, 8 sprat, 36 smelt, 2 cyprinids, 20 eelpout, 4 salmon, 2 trout, 1 ruffle, 1 three-spined stickleback and 2 common whitefish were consumed by grey seals. As herring made up the largest proportion of the relative numerical contribution (78 %) ( $N_i$ ), only smelt (10 %) and eelpout (6 %) contributed more than 5 % to their diet (Table 6).

Grey seals had also consumed other items such as plastics, rocks, pieces of wood, other plants and roe. Also, of the 73 grey seals, 47 contained parasitic nematode *Contracaecum osculatum*, either attached to the stomach tissue or among the stomach contents. The amount of these parasites was substantial in some of the stomachs with an average of 11.76 grams per stomach (range 0.05 - 69.05 grams) (only those nematodes that were not attached, were weighed).

**Table 6.** The frequency of occurrence ( $FO_i$ ), relative numerical contribution ( $N_i$ ), number of consumed individuals and number of otoliths for prey taxa recovered from grey seal stomachs, where n equals the number of seals used for the analysis.

n = 21					
Common name	Taxon	$FO_i$	$N_i$	No. of consumed ind.	No. of otoliths
Herring	<i>Clupea harengus</i>	76	78	274	544
Sprat	<i>Sprattus sprattus</i>	19	2	8	12
Smelt	<i>Osmerus eperlanus</i>	10	10	36	71
Cyprinids	<i>Cyprinidae</i>	5	1	2	2
Eelpout	<i>Zoarces viviparus</i>	5	6	20	40
Salmon	<i>Salmo salar</i>	5	1	4	7
Trout	<i>Salmo trutta</i>	5	1	2	3
Ruffle	<i>Gymnocephalus cernuus</i>	5	0	1	1
Common whitefish	<i>Coregonus lavaretus</i>	5	1	2	2
Three-spined stickleback	<i>Gasterosteus aculeatus</i>	5	0	1	4
Baltic macoma	<i>Macoma baltica</i>	5	0	1	
Unidentified bones		33			
<b>Total number</b>				<b>351</b>	<b>686</b>

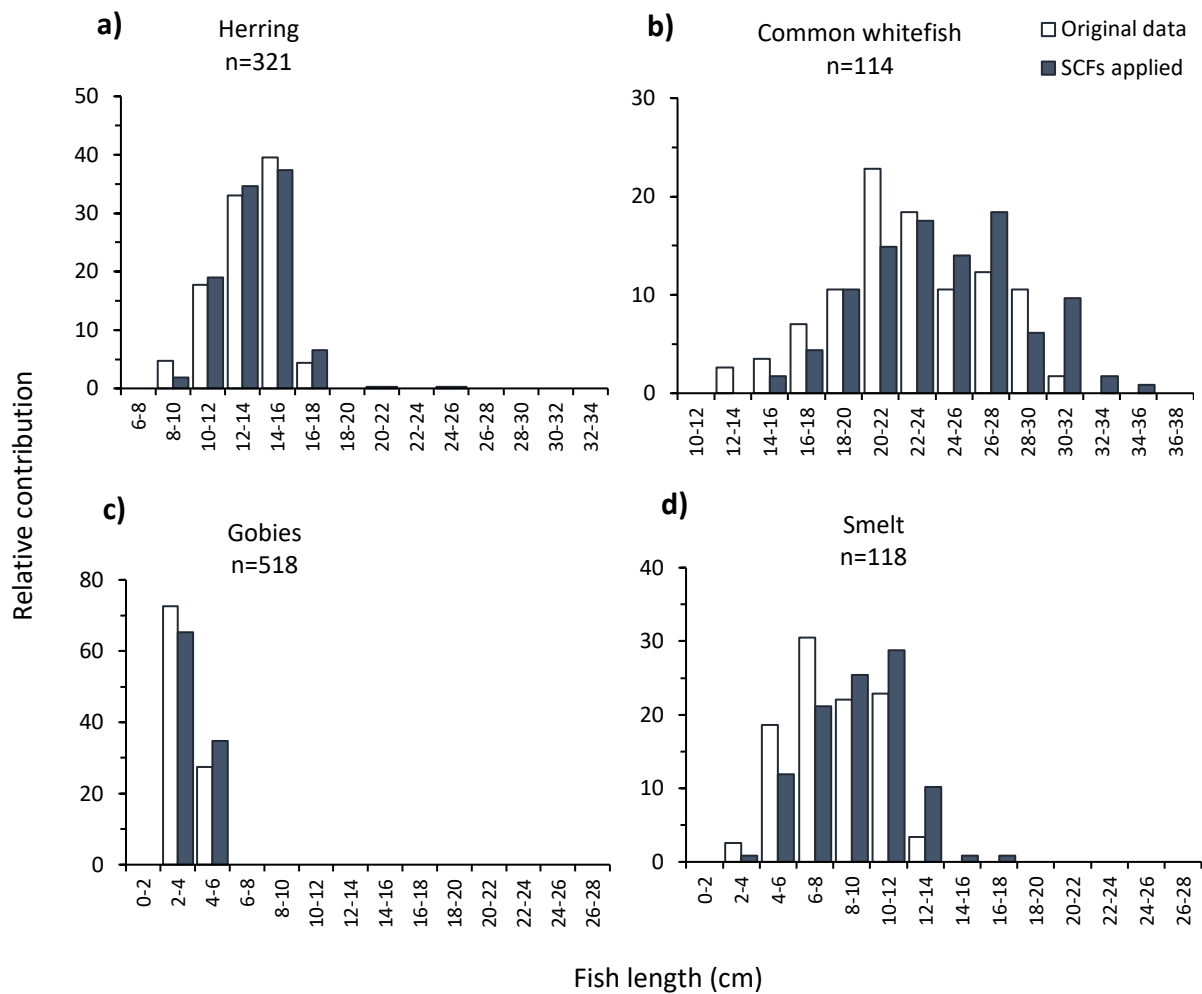


**Figure 7.** The proportion of grey seal stomachs containing each prey taxon ( $FO_i$ ) (light bars) and the proportion of each prey taxon in all identified taxa ( $N_i$ ) (dark bars) in the stomachs of grey seals hunted in 2017.

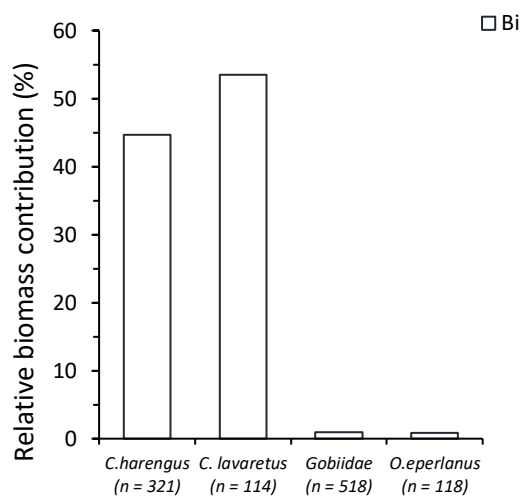
### 3.3. Prey size

The estimated fish lengths ranged from a goby of 2.3 centimeters (cm) to a common whitefish of 31.3 cm (SCFs not applied). Most of the herring lengths (90 %) were between 10 and 16 cm (median = 13.3 cm), all of the gobies between 2 and 6 cm (median = 3.4 cm) and most of the common whitefish (92 %; median = 22.1 cm) and smelt (94 %; median = 7.9 cm) between 16 and 30 cm, and 4 and 12 cm respectively (Figure 8). In comparison, when the SCFs were applied, the estimated lengths ranged from a goby of 2.4 cm to a common whitefish of 34.2 cm. Moreover, the proportion of larger fish increased among all four species with higher median, minimum and maximum lengths when SCFs were applied. The majority (92 %) of the estimated common whitefish lengths were now between 18 and 32 cm (median = 24.1 cm) and most of the smelt lengths (97 %) between 4 and 14 cm (median = 9.3 cm). More herring lengths were now between 16 and 18 cm, and gobies between 4 and 6 cm while the majority of both species remained the same as with the original data. Figure 8 shows the distribution of fish lengths for herring, common whitefish, gobies and smelt before and after SCFs were applied.

The total estimated biomass of the four most numerous species (herring, gobies, common whitefish and smelt) consumed by ringed seals was 21.1 kilograms and was dominated by common whitefish that made up the largest proportion (54 %) of the relative biomass contribution ( $B_i$ ). Due to its large body size, common white fish became the most important prey in terms of biomass instead of the smaller herring (most common fish species) or gobies (most numerous species). After common whitefish, herring were the next most important prey contributing 45 % to ringed seal diet, while gobies and smelt only 1 % each (Figure 9). As it was not possible to determine the original non-digested biomass of *Saduria entomon*, they were not included in this analysis. However as mentioned previously, *Saduria entomon* were the most common species recovered from ringed seals and if their total biomass (1027 g) were included, *Saduria entomon* would have made up 5 % of the relative biomass contribution.



**Figure 8.** Fish length distribution for herring, common whitefish, gobies and smelt based original data (light bars) and data with size correction factors (SCFs) applied (dark bars). The data was based on the prey remains recovered from ringed seal stomachs where  $n$  is the number of sagittal otoliths used for fish size estimation.



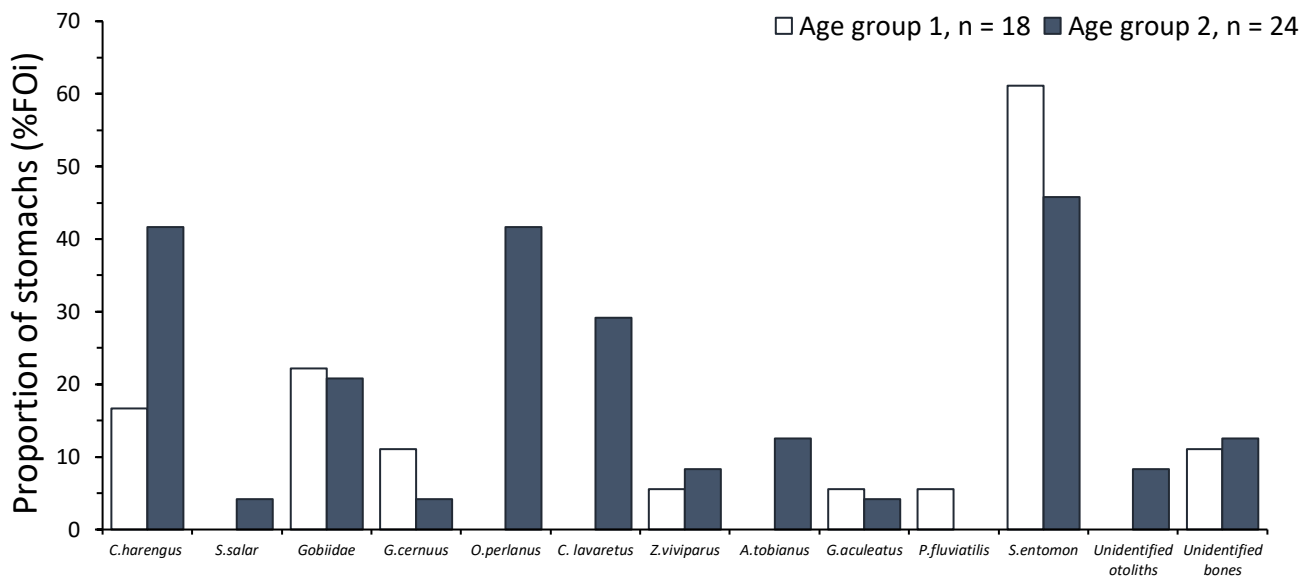
**Figure 9.** The relative biomass contribution of herring, common whitefish, gobies and smelt based on the estimated weights from the sagittal otoliths (SCFs applied) recovered from ringed seals, where  $n$  equals the number of otoliths used for fish weight estimation.



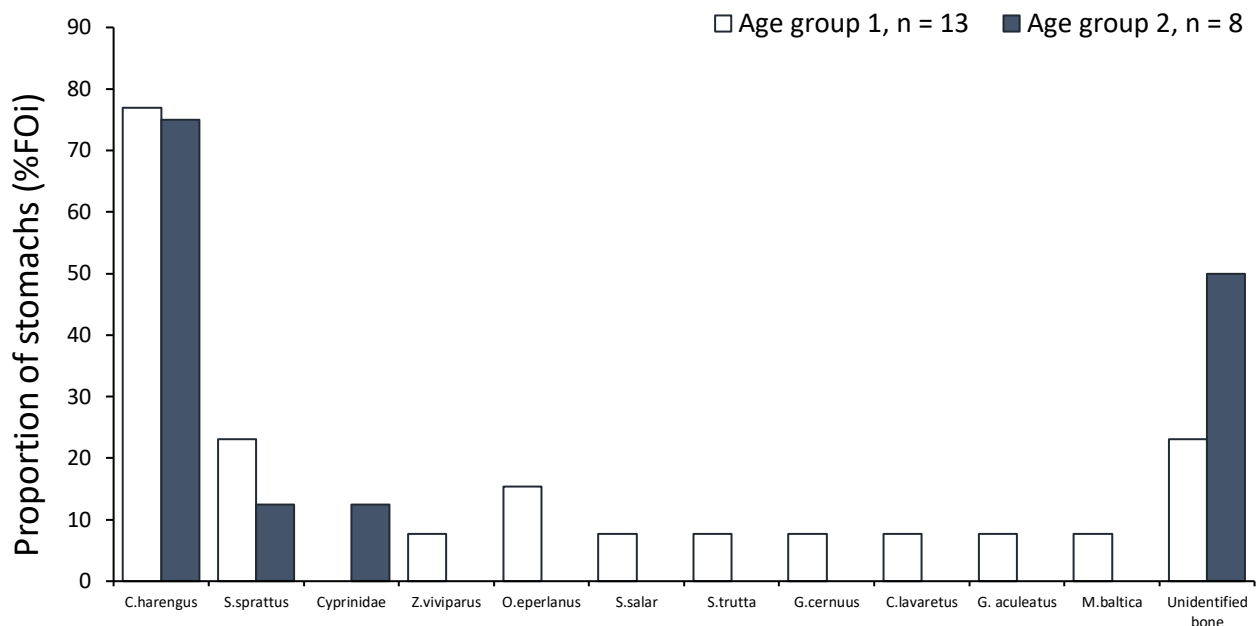
### 3.4. Diet composition variation

#### Age

The frequency of occurrence ( $FO_i$ ) of smelt and common whitefish were higher among ringed seals in age group 2 (2+ y.) compared to age group 1 (0 – 1 y.) (smelt:  $\chi^2 = 10$ ,  $df = 1$ ,  $P = 0.002$ ; common whitefish:  $\chi^2 = 7$ ,  $df = 1$ ,  $P = 0.008$ ) (Figure 10). Both species were also more numerous among mature seals (smelt: K-W:  $P = 0.004$ ; common whitefish: K-W:  $P = 0.024$ ). Furthermore, the amount (grams) of consumed *Saduria entomon* varied among age groups with mature seals containing more than younger seals (K-W:  $P = 0.014$ ). Other prey did not show significant differences between age groups ( $FO_i$ ). Moreover, the diversity index was higher for seals in age group 2 (1.46) compared to group 1 (0.89). In comparison, age group showed no significant effect on the frequency of occurrence of prey among grey seals (Figure 11). However, mature seals had consumed more herring compared to younger seals (K-Wallis:  $P = 0.015$ ) whilst the diversity index was higher for younger seals (1.22) than for mature seals (0.10).



**Figure 10.** The proportion of Baltic ringed seal stomachs of age group 1 (0 – 1 y.) and age group 2 (2 + y.) containing each prey item ( $FO_i$ ) in 2017.



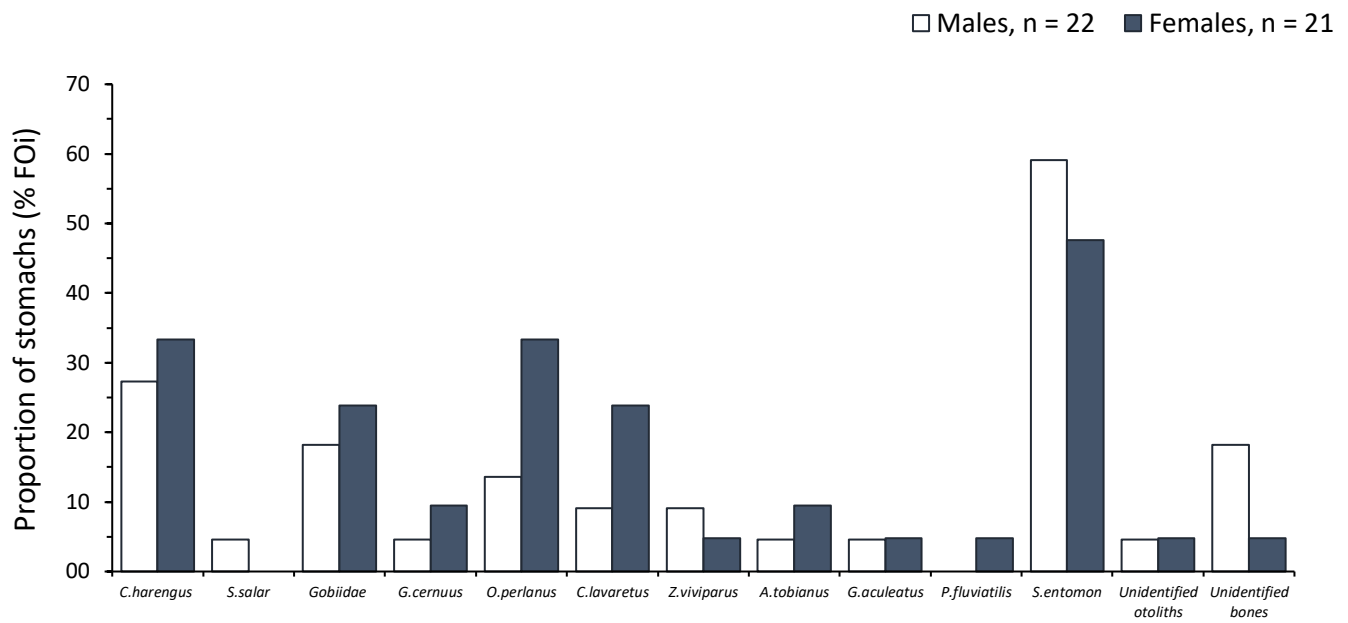
**Figure 11.** The proportion of Baltic grey seal stomachs of age group 1 (0 – 1 y.) and age group 2 (2 + y.) containing each prey item (FO<sub>i</sub>) in 2017.

## Sex

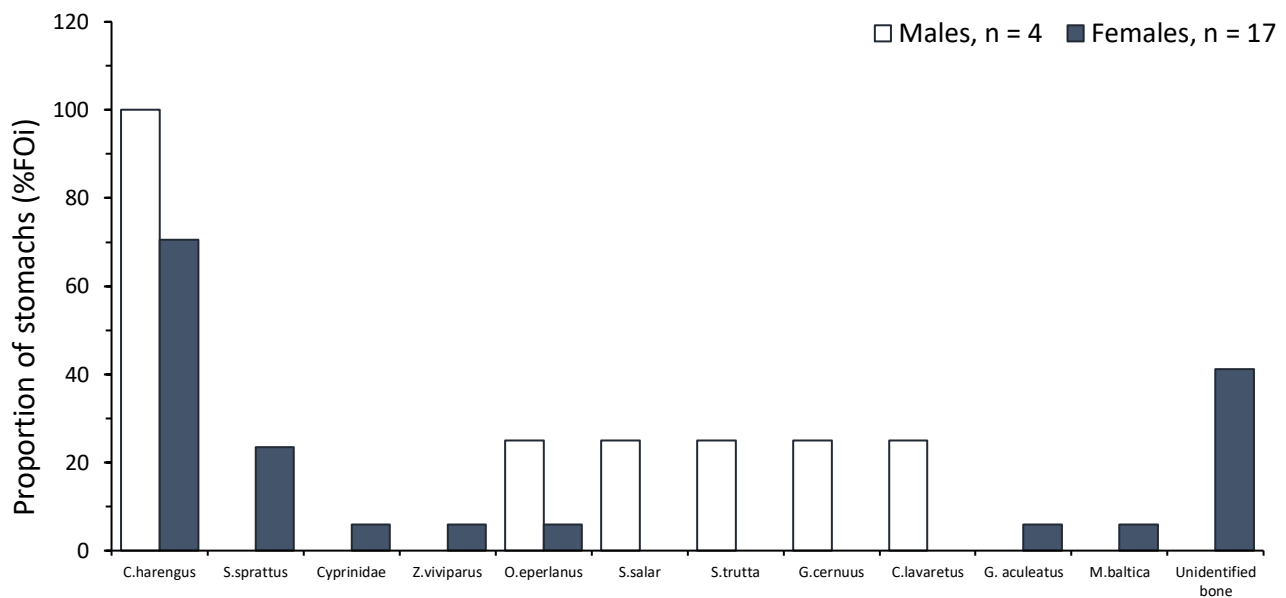
There were no significant differences in the frequency of occurrence or number of consumed prey items between sexes among ringed seals (Figure 12). The diversity index for females was slightly higher (1.43) than for males (1.22). However, herring and sprat occurred more frequently among female grey seals compared to males (herring:  $\chi^2 = 4$ ,  $df = 1$ ,  $P = 0.046$ ; sprat:  $\chi^2 = 4$ ,  $df = 1$ ,  $P = 0.046$ ). Also, the frequency of occurrence of unidentified bones was higher for females  $\chi^2 = 7$ ,  $df = 1$ ,  $P = 0.008$ ) (Figure 13.). Other prey indicated no significant differences between sexes among grey seals (FO<sub>i</sub>). The diversity index was higher for male (1.40) than for females (0.67).

## Geographical region

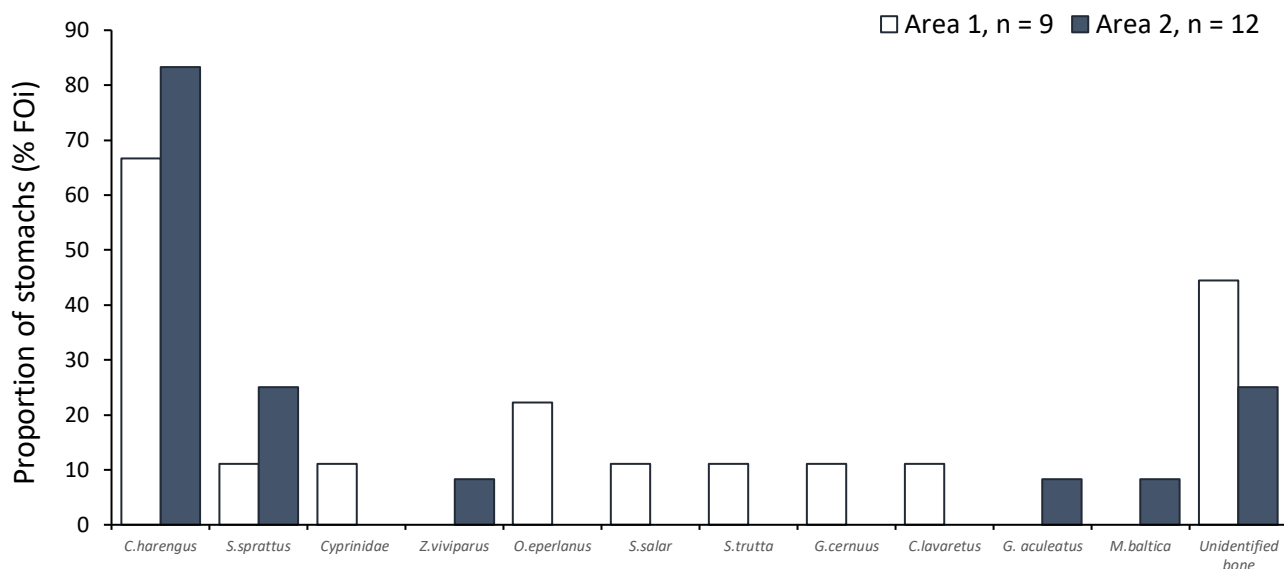
Geographical region showed no significant effect on the frequency of occurrence or number of prey individuals among grey seals (Figure 14). The diversity index was higher for seal from the Bothnian Bay and Bothnian Sea (1) (0.92) than for seals from the Archipelago Sea and Gulf of Finland (2) (0.54).



**Figure 12.** The proportion of Baltic ringed seal stomachs of males and females containing each prey item (FO<sub>i</sub>) in 2017.



**Figure 13.** The proportion of Baltic grey seal stomachs of males and females containing each prey item (FO<sub>i</sub>) in 2017.



**Figure 14.** The proportion of Baltic grey seal stomachs of area 1 and area 2 containing each prey item (FOI) in 2017.

### Prey size

The size of the fish consumed by ringed seals varied between demographic factors (i.e. age and sex) (Table 7). Males were significantly negatively correlated with the length of the consumed fish between individuals ( $P = 0.00101$ ). Age was also significantly correlated with the length of consumed fish between individuals ( $P < 0.01$ ). Moreover, according to this analysis, male seals had consumed smaller fish compared to females, whereas mature seals ( $2 + y.$ ) had eaten larger fish than younger seals ( $0 - 1 y.$ ).

**Table 7.** Results of the linear mixed model testing for the effects of age and sex on the size of consumed fish. Species (herring, common whitefish, gobies and smelt) taken into account as random effect.

	Estimate	Std. Error	t value	p
(Intercept)	2.24556	0.39111	5.742	<0.001
sexmale	-0.04988	0.01517	-3.288	0.00101
agegroupmature	0.08959	0.01836	4.881	<0.001

## 4. Discussion

### 4.1. Sample composition

This study was based on the seal samples collected and provided by seal hunters and made available by the National Resources Institute Finland Luke in 2017. Therefore, only a limited number of samples were available for examination. The initial dataset included 156 ringed and 73 grey seals of which 43 and 21 had consumed prey respectively. Seals were further categorized into groups based on age, sex and geographical region (grey seals only) resulting in rather small sample size for the analyses. Furthermore, not all groups were equally distributed which resulted in further uncertainties when interpreting the results. This was especially true for grey seals when comparing sexes, as the sample included only four males (Table 5). Furthermore, even though the animals were killed opportunistically with no particular selection process, the use of hunted animals introduces biases since hunted animals cannot be killed completely at random. This is generally because the seals' breeding and moulting locations are often known and since they are often shot near the fishing gear. Therefore, due to the small sample size and the sample collection method, it is important remember that the result of this study should be interpreted with caution.

As the annual open seal hunting season in Finland commences in April (16.4 - 19.4) (Suomen Riistakeskus 2019) and since most of the samples were collected in April and May 2017, the results of this study only represent the diet composition of Baltic ringed and grey seals in spring in Finnish sea area. It is widely known that the diet composition of seals varies between different seasons and that they reduce or cease foraging while breeding and moulting (e.g. Söderberg 1975, Lowry *et al.* 1980, Prime and Hammond 1990), which in Finland takes place between February and May (Helle 1938). Therefore, the underlying assumption here was that most of the stomachs would be empty or would contain only few prey remains. My results supported this assumption with only 28 % of the ringed and 29 % of the grey containing prey remains. Additionally, in order to interpret the results of diet studies to a larger temporal scale, more samples should be collected throughout the year.

This study was based on the prey remains, including otoliths, other hard particles and soft tissue remains recovered from ringed and grey seal stomachs. Most of the analyses were mainly based on the identification otoliths and the estimated number of prey individuals derived from them. This method can provide accurate information on the diet composition of seals and shed light on their recent diet history, however it also introduces biases. Some species are hard to differentiate

from each other, such as herring and sprat and common whitefish and vendace, due to the erosion of otoliths (Kauhala *et al.* 2011). Furthermore, small and fragile otoliths are often underestimated while the opposite is true for species with robust otoliths (Iverson *et al.* 2010). In general, digestion can cause severe biases when estimating the diet composition of seals by causing complete or partial digestion of otoliths. This erosion might affect the estimation of the number and size of consumed prey (e.g. Tollit *et al.* 1997, Bowen 2000). To avoid these biases, all prey recovered from both seals were taken into account instead of using just otolith when calculating the frequency of occurrence (FO<sub>i</sub>). Additionally, otoliths were measured, the most common otolith side (right or left) counted and otoliths were classified into erosion classes in order to avoid biases when estimating the original size of fish at ingestion (ringed seals only).

Furthermore, this study was only based on the analyses of the stomach contents instead of taking into account the entire gastrointestinal tract (i.e. stomach and intestines). Previous studies have suggested (e.g. Kauhala *et al.* 2011) that the use of intestines is not always necessary since the results from studies using both the stomach and intestine content have been very similar (based on the frequency of occurrence of prey species). Also, results might be more biased when using intestines, since digestion mainly occurs in the stomach (Frost and Lowry 1980, Harvey 1989, Pierce and Boyle 1991, Christiansen *et al.* 2005) and therefore the number of small otoliths, such as those of salmon (*Salmo salar*) might be lower in the intestines compared to the stomachs contents (Lundström *et al.* 2007). Moreover, it is important to consider all the possible biases when interpreting the results of this study and other studies based on the analyses from gastrointestinal tract contents.

#### **4.2. Prey occurrence and diet composition**

##### ***Ringed seal***

A benthic isopod *Saduria entomon* were the most common prey species consumed by Baltic ringed seals. Indeed, more than half (53 %) of the seals had eaten varying amounts of *Saduria entomon*, which are known to be an important prey species for ringed seals during breeding and moulting season since they are abundant and easily available for the seals to forage on (Söderberg 1975, Sinisalo *et al.* 2008). Previous studies have suggested that the differentiated dentition of ringed seals is also ideally suited for eating *Saduria entomon* (Helle 1983). The most common fish prey among ringed seals were herring that made up 30 % of their diet composition. Herring are known to

be the most important prey for ringed seals in the Baltic Sea (Söderberg 1975, Pöyhönen 2001), which was further confirmed by the finding of this study. Together the two most common species *Saduria entomon* and herring made up the majority of the diet (83 %), whereas other species contributed more numerically. This was especially true for gobies that were the most important species numerically, making up 54 % of the consumed prey individuals (n = 407). It is likely, that due to their small body size, seals need to feed on more individuals in order to fulfill their energy requirements compared to when consuming larger bodied species. Additionally, since ringed seals consume a variety of benthic and bottom dwelling species such as crustaceans and isopods and as gobies (e.g. sand goby) live on sandy bottoms in shallow waters, they are likely to play an important role in ringed seals' diet. It is, however, noteworthy that as goby otoliths were small and, in most cases, impossible to identify to species level they were analysed as a group (gobies). Sand goby is the most northerly ranging goby in the Baltic Sea, and therefore it is likely that a large proportion of the gobies recovered here were in fact sand gobies. To support this assumption, Suuronen and Lehtonen (2012) have also found sand gobies to be part of the ringed seal diet in the Bothnian Bay, where most of the seals for this study were hunted.

Other important species were smelt, three-spined stickleback and common whitefish. Smelt and common whitefish were also among the four most numerous fish species consumed together with gobies and herring. The importance of smelt seems to have increased compared to previous studies (Suuronen and Lehtonen 2012) where 39 individuals compared to the 67 in the present study were recovered. On the other hand, three-spined stickleback showed a contrasting pattern, with a decrease in their frequency of occurrence between Suuronen and Lehtonen (2012) (54 %) and this study (5 %). The importance of three-spined stickleback has been suggested to be higher toward the end of the summer and in autumn (Tormosov and Rezvov (1978), and thus my results support these findings. In addition, common whitefish occurred relatively frequently (16 %) with the majority (71 %) occurring among females. It is known that female seals require more energy during breeding and moulting and thus might have fed on common whitefish more frequently due to their fairly large body size. Furthermore, contrary to my results, Suuronen and Lehtonen (2012) did not find common whitefish but instead vendace in the ringed seal diet. Furthermore, no vendace were recovered in the present study. These differences might be explained by the fact that the species in the *Coregonus* family have very similar otoliths (Kauhala *et al.* 2011) and although all of these otoliths were identified as common whitefish instead on vendace in this study, this similarity introduces bias to the results. Previous studies have suggested that salmonids are not an important part of ringed seals diet in the Baltic Sea (Pöyhönen 2001, Stenman and Pöyhönen 2005, Suuronen

and Lehtonen 2012) and the results of this study found a paralleling trend as only one salmon was found, representing 2 % of the consumed prey. It is possible that due to the small size of ringed seals and in contrast the relatively large size of the salmonids, they rarely forage on Atlantic salmon and sea trout.

### ***Grey seal***

Herring were the most common and numerous prey species consumed by grey seals across the Finnish sea area. Also, according to previous studies (Söderberg 1975, Lundström *et al.* 2007 and 2010, Kauhala *et al.* 2011) herring have been the most important prey for grey seals in the Baltic Sea and furthermore, their importance in seal diet appears to have increased during the last decades. In fact, between 1968 and 1971 (Söderberg 1975) on average 24 % of the consumed prey were herring, whereas 57 % between 2001 and 2004 (Lundström *et al.* 2007), around 80 % between 2001 and 2007 (Kauhala *et al.* 2011) and 78 % in the present study. It has been suggested that this increase might be due to the decline in cod stock size in the Baltic Sea and to support this Lundström *et al.* (2007) found that the numerical importance of cod had decreased in grey seal diet from 19 % to 1 % between Söderberg's and their study. Furthermore, cod remains were not found in any of the grey seals in this study, which adds to the increasing evidence of dietary shift of the main prey species from cod to herring among Baltic grey seals. It is also likely, that herring dominating the diet is explained by the fact that most of the animals were hunted in April and May (90 %) during the annual grey seal moulting season, when seals are known to mainly prey on herring and thus have a more uniform diet compared to the rest of the year (Kauhala *et al.* 2011). The importance of other species in turn increases toward the end of the summer, when seals feed actively and begin to store energy for their next breeding (Hall and Thompson 2009).

Other important prey species were sprat and smelt. Similar to herring, the importance of sprat to grey seal diet seems to have increased since the late 1960s and early 1970s, which may be due to the increase in Baltic sprat stock (Thurow 1997, ICES 2004, Lundström *et al.* 2007). Furthermore, Söderberg (1975) found that on average 3 % of the consumed prey were sprat, whereas more recent study by Lundström *et al.* (2007) found that 11 % were sprat. The results of this study show, that after herring, sprat was in fact, the most common species consumed by grey seals, however, only 2 % of the consumed prey individuals were sprat. Moreover, sprat contributed more to the diet in the Gulf of Finland and the South West archipelago (Area 2), although the difference was not statistically significant. This, however, supports the findings of previous studies



(Kauhala *et al.* 2011), where sprat was found to be more important for grey seals in the southern Finnish sea area due to their more southern geographical range (Parmanne 1998). Additionally, smelt were the second most numerous species consumed by grey seals. This might be explained by their high abundance in the northern Baltic and the Bothnian Bay and the fact that smelt is a coastal schooling species (Shpilev *et al.* 2004), thus making it ideal prey for grey seals. Furthermore, all the smelt recovered in this study were from seals from the Bothnian Bay and the Bothnian Sea and Northern Quark (Area 1). Other prey species did not contribute significantly to grey seal diet. It is also noteworthy that all of the other species found: salmon, trout, ruffe and common whitefish, cyprinids, three-spined stickleback and eelpout were all recovered from one young seal (0 -1 y.).

#### **4.3. Prey size**

In order to avoid biases in prey size estimation, previous studies have explored and applied size correction factors to take into account erosion in the digestive tract (e.g. Prime and Hammond 1990, Tollit *et al.* 1997). Although published species-specific correction factors exist for some of the species found in this study, I estimated SCFs as the ration between average otolith size of erosion class 1 and erosion class 2 and 3 respectively, for the four most numerous species consumed by ringed seals following Lundström *et al.* 2007. The estimated fish lengths and the proportion of larger fish increased when SCFs were applied among all four species (i.e. herring, common whitefish, smelt and gobies). Therefore, since the prey size changed with similar degree and in the same direction for all four species, the diet composition did not change markedly. Since the size distribution of consumed prey changed toward larger and therefore older fish, applying such size correction factors has a significant effect increases the size overlap with commercially important fish such as herring and common whitefish (Lundström *et al.* 2007). The size of the consumed fish individuals ranged from a small goby of 2.4 cm to a large bodied common whitefish of 34.2 cm. It is, however, worth noting that seals often discard the head of larger fish before consumption and therefore the number of larger fish is often underestimated when analysing recovered otoliths (Lundström *et al.* 2007). Additionally, the total estimated biomass was dominated by common whitefish that made up the largest proportion (54 %) of ringed seal diet in terms of biomass. This is likely due to its large body size compared to for example, small gobies, that were the most numerous species consumed and herring that was the most common fish prey among ringed seals. After common whitefish, herring were the next most important prey contributing 45 % to ringed seal diet. Furthermore, *Saduria entomon* were the most common prey found in ringed seals, but

since it was not possible to determine the original non-digested biomass, they made up only 5 % of the relative biomass contribution.

#### **4.4. Diet composition variation**

##### **Age**

Older ringed seals (2+ y.) had consumed more smelt, common whitefish and *Saduria entomon* compared to younger seals (0 -1 y.). Mature seals had also consumed smelt and common whitefish more frequently. Indeed, 42 % of the mature seals had consumed smelt and 29 % common whitefish whereas none of the younger seals had eaten neither species. It is possible that these differences in diet composition between mature and younger seals are because mature seals might be more selective and prefer larger bodied fish such as common whitefish and abundant schooling fish like smelt (Shpilev et al. 2004), whereas younger seals consume a more varied diet (Beck *et al.* 2007). Furthermore, age did not appear to affect the composition of other prey species in ringed seal diet. The diversity index, however, showed higher species richness among older seals. As previously discussed, younger seals are generally thought to consume more diverse diet due to their inexperience (Beck *et al.* 2007) but interestingly the results of this study show the contrary. However, due to low sample size in the current study, these results may be biased and must be interpreted carefully.

Age did not have an effect on the frequency of occurrence of prey among grey seals, however, mature seals had consumed more herring compared to younger seals. Most of the older grey seals in this study were females (88 %), therefore the observed differences might be due to higher energy requirements of females during the breeding and moulting season, when they might be more selective in their foraging than males (Beck *et al.* 2007). Additionally, the results of the diversity index for grey seals supported the findings of earlier studies (Beck *et al.* 2007), with the index being higher for inexperienced younger seals that consume more varied diet than mature seals.

## **Sex**

As both female and male ringed seals are similar in size, the average diet composition between the sexes can be expected to be somewhat equal. Indeed, the results of this study indicated no significant differences in the diet composition between the sexes. In comparison, herring and sprat occurred more frequently among female grey seals, whereas males had consumed more varied diet. Since grey seals exhibit distinct sexual dimorphism (Bowen *et al.* 2003), it is expected to affect the dietary preferences and thus the diet composition. Additionally, as previously described, female grey seals require more energy during the breeding and moulting season compared to males, which might affect their foraging and diet composition. Furthermore, in Canada, male grey seals have been shown to consume less energy rich prey and more varied diet during spring compared to females (Beck *et al.* 2007). It should be noted however, that the number of grey seals in this study was limited and the results of the analyses should not be considered conclusive.

## **Geographic location**

I found no significant differences in the diet composition of grey seals between the two geographic regions. However, since the Baltic Sea is a brackish waterbody, where salinity decreases north toward the Bothnian Bay and in comparison, increases south toward the Danish straits, the abundance of freshwater and marine species varies between regions and thus differences in prey availability could lead to differences in diet composition of seals originating from different areas (Ojaveer *et al.* 2010). Therefore, it is likely that differences do exist, but due to the small sample size, my results are not conclusive and further research is needed. However, the composition of the grey seal diet in the Bothnian Bay and Bothnian Sea varied more than in the Archipelago Sea and Gulf of Finland. It is worth noting that this might be largely due to one seal from the Bothnian Bay that had consumed up to six different species while most of the seals had only consumed one species.

## **Prey size**

The results from the linear mixed model analysis indicated differences in the size of the fish consumed by ringed seals between demographic factors (i.e. age and sex) (Table 7). Males had consumed smaller fish compared to females, whereas mature seals (2 + y.) had eaten larger fish than younger seals (0 – 1 y.). These results supported the findings of the frequency of occurrence

and numerical contribution analyses, where mature ringed seals had consumed more and more frequently of smelt and common whitefish. Moreover, mature ringed seals appear to also consume larger fish than younger seals. Additionally, contrary to the results from the frequency of occurrence analysis, where no significant differences were found between sexes, the negative correlation between sex and consumed fish size was strong ( $P = 0.00101$ ). Female seals had consumed larger fish compared to males, which supports the findings of previous studies, where females have been suggested to consume more energy rich diet during breeding and molting season than males (Söderberg 1975, Beck *et al.* 2007).

## 5. Conclusions

The aim of this study was to provide more accurate and current information on the diet composition of Baltic ringed and grey seals in the Finnish sea area. The diet composition of ringed seals were dominated by benthic isopod *Saduria entomon*, that were the most commonly consumed prey. Herring were the most common, gobies the most numerous and common whitefish the most important fish prey in terms of biomass in ringed seal diet in the Bothnian Bay. Herring were the most important and the most common prey for grey seals. Other important prey were sprat and smelt, although herring contributed the most to their overall diet. Other prey did not contribute substantially to grey seal diet composition in the Finnish sea area. In addition, the diet composition varied between demographic factors (i.e. age and sex). Mature ringed seals had consumed more smelt, common white fish and *Saduria entomon*, compared to younger seals. Smelt and common whitefish also occurred more frequently among older ringed seals. Furthermore, mature grey seals had eaten more herring compared to younger seals. This difference in diet composition between age groups is likely due to the larger energy requirements of older seals, especially during breeding and moulting season compared to those of pups and juveniles. The frequency of occurrence of herring and sprat as well as unidentified bones were higher among female grey seals, which might be explained by the fact that females might be more selective toward their diet during breeding and moulting season, when their energy requirements have increased. Differences in the estimated size of the fish between demographic factors also occurred among ringed seals. Females had consumed larger fish compared to males, whereas mature seals had eaten larger fish than younger seals. A parallel trend was found between the diet composition analyses, indicating that mature as well as female ringed seals generally consumed more and larger prey than younger seals and male seals. Females had consumed larger fish compared to males, whereas mature seals had eaten larger fish than younger seals. The result of the analyses for grey seals had similar results with female seals

consuming more food. The geographical area did not appear to have any effect on the diet composition of grey seals.

The results of this study have provided more current information on the diet composition of Baltic ringed and grey seals in the Finnish sea area. However, in order to mitigate the increased seal-inflicted problems to coastal fisheries and to achieving sustainable and effective seal management and conservation, more information on the diet of Baltic seals is still needed. More knowledge on the biomass contribution and age of consumed prey should be acquired in the future to assess the severity of the seal-fishery conflict. Combining other methods together with the identification of recovered prey remains from gastrointestinal tract contents should be utilized to get the most representative estimation of the diet composition. Furthermore, using other correction procedures such as numerical correction factors when analysing otoliths would reduce biases caused by digestive erosion. There is yet much to be learned from the Baltic ringed and grey seals and in order to guarantee a sustainable future for the seals and the fishing industry in Finland, further investigation on the diet composition and foraging behaviour of the seals is needed in the future.

## **6. Acknowledgements**

This thesis was done at the University of Helsinki, under the supervision of Dr. Kaarina Kauhala (Natural Resources Institute Finland Luke) and professor Jukka Horppila. I would like to thank both my supervisors for the support and advise every step of the way, but especially Dr. Kaarina Kauhala for the trust and this incredible opportunity. I am also forever grateful to Dr. Jari Raitaniemi, professor Kari Nyberg, professor Jyrki Lappalainen and professor Hannu Lehtonen for the endless help and advice on fish and otolith identification and processing. I would also like give thanks to Petri Timonen for the preparation of the seal samples and all the personnel at the Ohtaoja research station (Luke) for the support and the best introduction to sample collection. I also want to thank all the personnel at Natural Resources Institute Finland Luke, who were part of the age, sex and species determination of the seal samples. Lastly, I wish to thank all the hunters who collected the material for this study.

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